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# THE FLOW OF WATER INTO THE DEEP SEA BASINS OF THE WESTERN SOUTH PACIFIC OCEAN

By K. Wyrtki*

[*Manuscript received October* 25, 1960]

*Summary*

The hydrographic conditions in the deep sea basins of the western South Pacific Ocean are analysed using relations between potential temperature and salinity, based on observations made from H.M.A.S. *Gascoyne* in 1960. It is shown that the bottom waters in the Coral Sea Basin and in the Solomon Basin are both characterized by a comparatively high salinity and that they come from the East Australian Basin. The bottom waters in the New Hebrides Basin, the New Caledonia Trough, and the Fiji Basin come from the central Pacific Basin. The water in the New Hebrides Basin and that in the New Caledonia Trough both have a slight admixture of water of higher salinity which has escaped over the ridges on the east sides of the Coral Sea Basin and the Solomon Basin. The Coral Sea Basin and the Solomon Basin considered as a unit is an example, probably the unique case, of the inflow into a basin occurring at a higher level than the outflow. The sill depths of the different basins are determined by using potential temperature characteristics. The water exchange of the Coral Sea Basin is discussed theoretically. The upward velocity at depths between 3000 and 4000 m is of the order of $1 \cdot 5 \times 10^{-5}$ cm/sec and the rate of inflow 0·04 million $m^3$/sec.

## I. Introduction

From February to April 1960, H.M.A.S. *Gascoyne* worked 97 hydrographic stations from the surface to the bottom in the area between Sydney, North Cape of New Zealand, Fiji, the Bismarck Archipelago, and the east coast of Australia. The data from these stations were used in an analysis of the flow of deep water and of the exchange of bottom water in the various basins.

## II. The General Topography of the Region

The position of the 3000 m isobath, shown in Figure 1 (copied with only a few modifications from the General Bathymetric Chart of the Oceans, Sheet A'III) gives a general impression of the subdivision of the ocean bottom in this region. The *East Australian Basin*, situated between the Australian east coast and the Lord Howe Ridge, extends to about 55° S. It has an average depth of about 4600 m with several depressions of more than 5000 m. In the south it is connected with other basins around the Antarctic continent at depths greater than 3500 m, thus enabling the Deep and Bottom Water to enter. A narrow channel with depths exceeding 3000 m extends from the East Australian Basin north towards the Coral Sea, leading at approximately 18° 30′ S. over two sills of slightly less than 3000 m depth into the Coral Sea Basin.

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The *Coral Sea Basin* has an abyssal plain with depths ranging from 4400 to 4800 m. The General Bathymetric Chart shows a channel with a depth of more than 3000 m extending to the east from this Basin. More recent soundings entered on British Admiralty Chart No. 208 indicate that this connection is not as deep,

Fig. 1.—Deep sea basins of the western South Pacific Ocean. The flow of bottom water is indicated by arrows, the shape of the basins is indicated by the 3000-m line. Positions of stations mentioned in text are shown.

and that the Coral Sea Basin may be closed in the vicinity of this connection at a depth of about 2800 m. However, the latter chart shows, east of the Pocklington Islands, a channel running towards the north, which is not shown in the General Bathymetric Chart. According to the few available soundings, this channel could be as

deep as 3800 m, and is therefore the deepest connection from the Coral Sea Basin to any other basin.

The *Solomon Basin* is surrounded by the Solomon Islands, New Britain, New Guinea, and the Louisiade Archipelago. It is subdivided into two basins by a ridge with a sill depth of about 3600 m, running from Woodlark Island towards New Georgia. The northern basin includes the Bougainville–New Britain Trench with the Planet Deep (9140 m). The eastern basin is only about 4600 m deep. The deepest connection of the Solomon Basin with the central Pacific Ocean is over a sill south of New Georgia; this sill is not shown on the General Bathymetric Chart. Recent soundings, and the soundings shown on British Admiralty Chart No. 214 and the U.S. Hydrographic Office Chart No. 5912, indicate that a ridge extends southwards from New Georgia to a larger plateau situated in about 10° to 11° S. and 157° to 158° E. of which the highest portions rise to less than 1000 m. The sill depth of this ridge is about 3000 m. The passage between Bougainville and New Ireland has a sill depth of about 2600 m.

A deep trench, situated south of Guadalcanal and of San Cristobal, bends northwards to the east of San Cristobal. A sounding of 7315 m is shown on the British Admiralty Chart No. 208 south of San Cristobal and a sounding of 7400 m (uncorrected) was obtained to the south-east of that island. No similar depths are shown on the General Bathymetric Chart. It seems appropriate to name this the San Cristobal Trench. It seems to be directly connected, at a depth of somewhat less than 5000 m, with the central basin of the Pacific Ocean.

The *New Hebrides Basin* is situated between the New Hebrides and New Caledonia, and extends to the north of the latter. The greatest depth is 7660 m and is in its south-eastern part. The General Bathymetric Chart shows this basin connected at depths greater than 4000 m with the central Pacific, but recent soundings by the R.A.N. Hydrographic Office indicate that there may be a ridge at approximately 13° 30′ S. with a sill depth of the order of 3000 m.

The *New Caledonia Trough* is situated between the Lord Howe Ridge and the Norfolk Ridge, and runs in a general north–south direction from New Caledonia to New Zealand. The greatest recorded depth is 4005 m and is south of New Caledonia. North-west of that island the trough is connected with the New Hebrides Basin at depths of about 3000 m. Towards the south the trough becomes shallower with depths of about 2300 m in its centre. West of New Zealand a narrow, northwards bent connection runs to the Fiji Basin at a depth of about 2050 m. Another connection runs to the East Australian Basin in about 23° S. south of the Chesterfield Reefs. The sill depth of this channel is at approximately 2300 m.

The *Fiji Basin* extends between the Fiji Islands and New Zealand, and has a depth of about 4500 m except where a few soundings of 5000 m have been recorded. The Fiji Basin is closed in the west by the Norfolk Ridge, having only a narrow connection 2050 m in depth with the New Caledonia Trough. In the east the basin is closed by the Kermadec Ridge, running northwards from New Zealand, and by the South Fiji Ridge connecting to the Fiji Islands. The sill depth of this ridge north and south of the Kermadec Islands seems to be less than 2500 m (Brodie and

Hatherton 1958). In the north this basin is closed by a ridge running from Fiji south-west towards Conway Reef and Hunter Island. Between these two islands the ridge seems to have two thresholds of approximately 3000 m depth, and the sea bed north of the ridge is of similar depth. Another connection exists towards the New Hebrides Basin near 21° S., 169° E.; the soundings in its vicinity are too few to determine the sill depth between the two basins, but it seems to be greater than 3000 m. The Fiji Basin includes two smaller basins, the Norfolk Basin to the north-west, and the Havre Trough to the north-east of New Zealand.

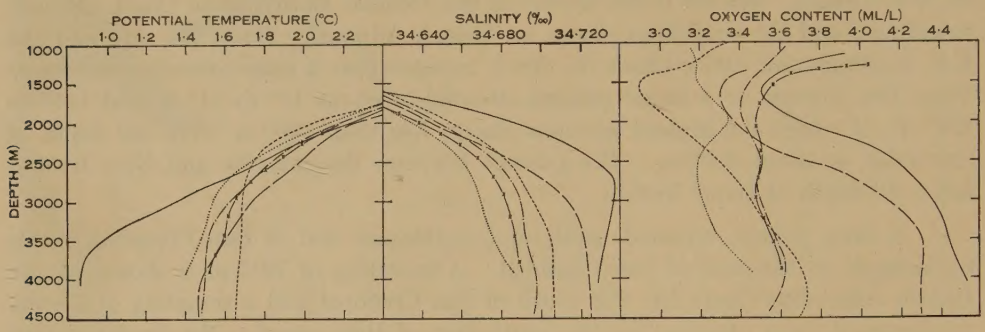


Fig. 2.—Vertical distribution of potential temperature, salinity, and oxygen content below 1000 m depth at selected stations.

———— G2/90/60 East Australian Basin ····· G2/59/60 Central Pacific Basin
— — — G2/134/60 Coral Sea Basin —·—·— G2/74/60 New Hebrides Basin
- - - - - - - - G2/169/60 Solomon Basin —×—×— G2/36/60 Fiji Basin

For positions of individual stations see Figure 1.

## III. The Observations

The hydrographic data used in this paper are recorded in C.S.I.R.O. Aust. (1961). Temperatures were measured with standard reversing thermometers giving an accuracy of $\pm 0{\cdot}02$°C. The salinities were determined with an inductivity-coupled salinometer giving an accuracy as high as $\pm 0{\cdot}003$‰ (Brown and Hamon 1961). The high precision of the determinations made by this instrument allowed conclusions to be drawn regarding the spreading of water in the various basins, which would not have been possible from an analysis of temperature only, or from salinity determinations made by the traditional chlorinity titration method.

## IV. The Vertical Structure of the Water Masses

The salinity minimum (34·50‰) of the Antarctic Intermediate water is found at the 1000 m level in the whole region. Below that level the salinity increases steadily to above 34·65‰, and the temperature decreases. The oxygen content, which is comparatively high at 1000 m, shows a distinct minimum (2·7–3·5 ml/l) between 1500 and 2000 m depth. This oxygen minimum marks approximately the boundary between the Intermediate and Deep Water. Vertical curves of temperature, salinity, and oxygen content are given in Figure 2 for different parts of the region.

The bottom topography suggests that the conditions in the East Australian Basin and in the central Pacific Ocean can be used to explain this flow. The distribution of properties in the East Australian Basin, represented by Station G2/90/60 (Fig. 2) shows that below 2000 m the values for salinity as well as for oxygen content are the highest in the region. The weak salinity maximum (34·730‰) at about 3000 m indicates the position of the Deep Water, and can be interpreted as a last trace of the North Atlantic Deep Water, which is characterized by a salinity maximum (Wüst 1935; Stommel and Arons 1960). Slightly lower salinities and lower temperature deeper than 3500 m are representative of the Antarctic Bottom Water.

The distribution of properties in the central Pacific Ocean, represented by Station G1/59/60 north of the New Hebrides, shows that the values for salinity as well as for oxygen content below 2500 m are the smallest in the region. Water with these properties ascends slowly from the Pacific abyss, and consequently has properties similar to those of the Pacific Bottom Water. Wooster and Volkmann (1960) have shown that Pacific Bottom Water is a branch of Antarctic Bottom Water, which enters the Pacific Ocean south of New Zealand. It is identical in origin with the bottom water in the East Australian Basin.

The curves for vertical distribution of salinity and oxygen content (Fig. 2) indicate that the values for all other basins in the region fall between the curves for the East Australian Basin and the central Pacific Ocean. It is therefore concluded that the bottom water of the basins is derived from these two source regions. The potential temperatures in all other basins are higher than those at Stations 59 and 90, indicating that the communication to these basins is interrupted at higher levels than that to the two source regions.

## V. Salinity and Oxygen Content at a Potential Temperature of 1·8°C

The distribution of properties at a depth slightly above the sill depths of most of the basins is used to explain the flow of deep water and its penetration into the various basins. These sill depths are of the order of 3000 m, as shown in Section II. However, plots of properties such as temperature, salinity, and oxygen content at a given depth may show variations resulting from vertical displacements of the different layers, and this may thus lead to inconsistencies in the pattern of isolines. Consequently, in this paper, salinity and oxygen content have been plotted, not at a given depth, but as interpolated from vertical curves at the potential temperature of 1·8°C. The depth of this isotherm ranges from 2300 to 2800 m in the region.

The salinity values at a potential temperature of 1·8°C (Fig. 3) are highest (above 34·73‰) in the East Australian Basin. They decrease towards the north and in the Coral Sea Basin they are slightly above 34·700‰ in the west and slightly below in the east. A further decrease occurs towards the Solomon Basin and towards the east. The values below 34·670‰ in the northern part of the Solomon Basin are probably caused by an inflow of water at near 2000 m from the central Pacific Ocean through the passage between Bougainville and New Ireland. The lowest values (less than 34·660‰) appear to the north and east of the New Hebrides and are characteristic of conditions in the central Pacific Ocean. These lower values extend south into the Fiji Basin and to a lesser degree into the New Hebrides Basin.

In the New Caledonia Trough the values are all between 34·682 and 34·689‰, that is practically within the accuracy of the salinity determination.

A similar pattern is shown by the distribution of oxygen content at a potential temperature of 1·8°C (Fig. 4). The highest values are found in the East Australian

Fig. 3.—Distribution of salinity at a potential temperature of 1·80°C in the western South Pacific Ocean. The depth contour of 2500 m is shown. The individual stations are indicated, the numbers give the thousandths of the salinity value above 34·000‰.

Basin with more than 4·0 ml/l; they decrease to less than 4·0 ml/l in the Coral Sea Basin. The lowest values of less than 3·2 ml/l are found in the northern part of the Solomon Basin and north and east of the New Hebrides, and represent the water of the central Pacific Ocean. From there the oxygen content increases slightly towards the south, in the Fiji Basin as well as in the New Hebrides Basin.

## VI. The Properties of the Water in the Basins

An analysis of the water masses in the various basins is made, using temperature–salinity relations. As observations at different depths have to be compared, the potential temperature has to be used, even if doubts about the accuracy of the

Fig. 4.—Distribution of oxygen content at a potential temperature of 1·80°C in the western South Pacific Ocean. The depth contour of 2500 m is shown. The individual stations are indicated together with the oxygen content in ml/l.

determination of the coefficient of thermal expansion have been raised recently (Cochrane 1959). Three diagrams have been prepared, combining the data from the basins affected by water from the East Australian Basin, by water from the central Pacific Basin, and for the area of mixing between these two. The stations in the different basins are grouped; their positions are shown in Figures 3 and 4 and individual stations referred to are shown in Figure 1.

Figure 5 combines the observations from the East Australian Basin, the Coral Sea Basin, and the Solomon Basin. In the East Australian Basin the salinity values are highest at all depths or potential temperatures. They show a weak maximum

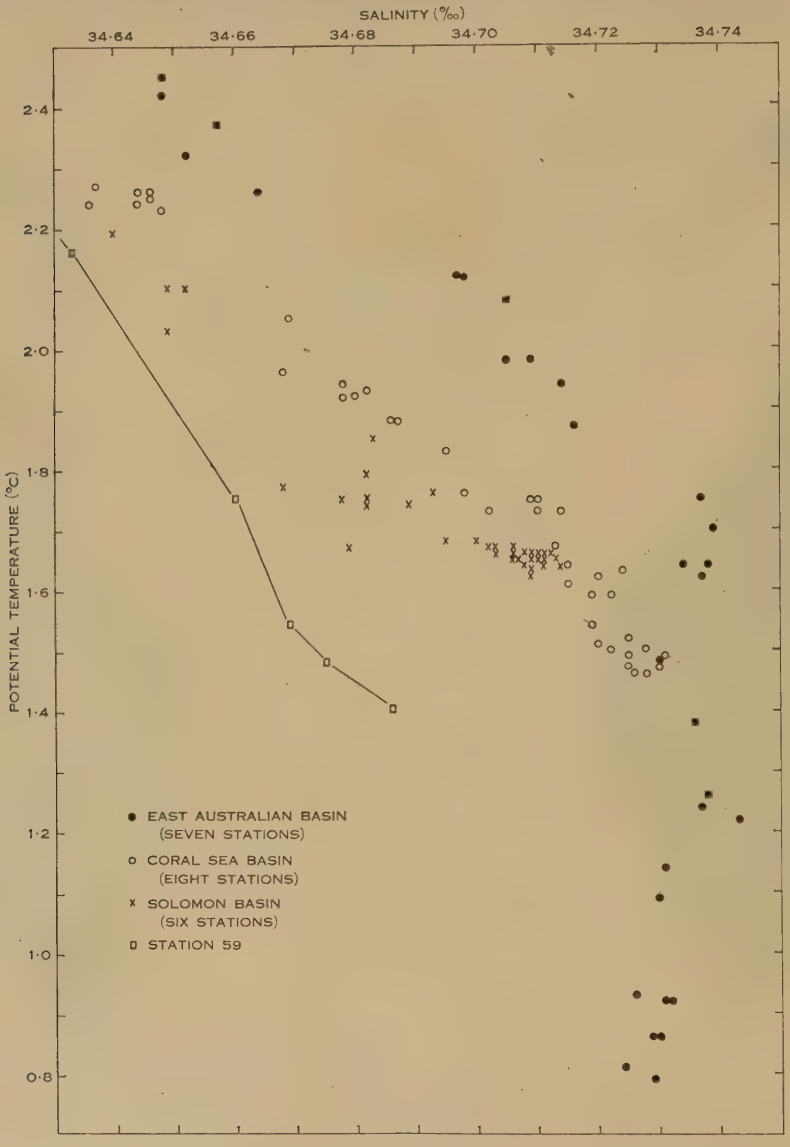


Fig. 5.—Potential temperature–salinity diagram for stations in the East Australian, Coral Sea, and Solomon Basins. For position of individual stations see Figure 1.

at potential temperatures between 1·6° and 1·2°C, corresponding to a depth of about 3000 m. Below this maximum the values decrease again to less than 34·735‰. A temperature minimum is usually found near 4000 m, but the potential temperatures

decrease, reaching less than 0·80°C at the bottom. As the sill depth between this basin and the Coral Sea Basin is at about 3000 m (Section II), water from the layer of the salinity maximum must enter the Coral Sea Basin. In Figure 5 the potential temperature–salinity values of the bottom water in the Coral Sea Basin indicate clearly that this water is derived from the salinity maximum outside the basin. The highest salinity found in the Coral Sea Basin is 34·731‰, the lowest potential temperature is 1·46°C. In the Coral Sea Basin there is usually a temperature minimum at about 4000 m depth, but below this depth the potential temperature remains constant within the accuracy of the measurements. A comparison of the potential temperature in the two basins (Fig. 2) determines the sill depth between them at 2850 m, a value fully consistent with soundings so far available.

Although water from the salinity maximum in the East Australian Basin can enter the Coral Sea Basin and fill its deepest portions, the rate of its ascent in the basin is slow enough to allow effective mixing with the water at higher levels. In the layer between 4000 m and the sill depth (2850 m) the temperature is increased and the salinity decreased (Fig. 2) owing to interaction with water above. Thus at 2850 m the potential temperature has risen to 1·79°C and the salinity has decreased to 34·708‰ in contrast to values of 1·46°C and 34·736‰ in the same depth outside the basin.

Because the bottom water in the Solomon Basin (Fig. 5) has almost the same characteristics (a potential temperature of 1·64°C and a salinity of 34·711‰) as the water in the Coral Sea Basin between 3000 and 3500 m depth, it must come from there. The potential temperature of 1·64°C is found in the Coral Sea Basin at a depth of 3400 m, so it must be assumed that the deep narrow channel connecting the Coral Sea Basin and the Solomon Basin is 3400 m deep (see Section II). The sill between the Solomon Basin and the central Pacific Basin is approximately 3000 m deep, so the Pacific Deep Water has no part in the formation of bottom water in the Solomon Basin. This is shown in the potential temperature–salinity curve (Fig. 5) of Station 59 north of the New Hebrides. The comparatively high salinity values in the Solomon Basin cannot be explained by the entry of water from the central Pacific Basin, although at higher levels the effect of water from the central Pacific Ocean can be easily recognized from the tendency of the salinities in the Solomon Basin to approach those at Station 59. This influence is strongest at potential temperatures of about 1·70°C, corresponding to a depth of about 2600 m, which is just the sill depth of the passage between Bougainville and New Ireland, and must be the point where the inflow occurs of water of lower salinity from the central Pacific Ocean, as is shown in Figure 3. However, it is unexpected that the water above 3000 m is colder in the Solomon Basin than it is in the Coral Sea and this can be explained by inflow of water from the central Pacific Ocean at about 2600 m depth. Because this water has a potential temperature of 1·67°C, which is only 0·03° higher than the bottom water, it cannot cause any downward flow of heat, which could increase the temperature in layers below 3000 m. As a consequence the potential temperature is almost constant from 3000 m to the bottom.

The potential temperature–salinity relation of nine stations south of the sill at 13° 30′ S. inside the New Hebrides Basin, is shown in Figure 6. The salinities

and temperatures of the bottom water in this basin are slightly higher than those at Stations 58 and 59, which are outside the basin and are characteristic of the deep water in the central Pacific Basin. It is therefore assumed that the bottom water in the New Hebrides Basin is a mixture of central Pacific deep water and water of higher salinity from the Coral Sea Basin. The characteristics of the water in the Coral Sea Basin are represented by Station 186 (Fig. 6). Station 181 in the San Cristobal Trench has almost the same potential temperature–salinity relation as Station 186 in the

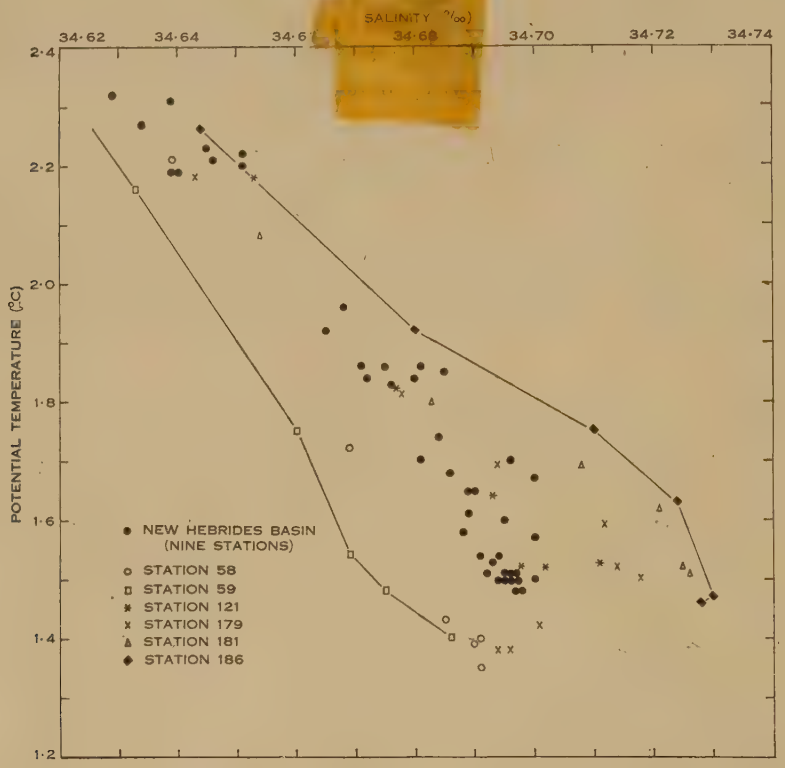


Fig. 6.—Potential temperature–salinity diagram for stations in the New Hebrides Basin and San Cristobal Trench. For position of individual stations see Figure 1.

Coral Sea, thus indicating that water leaves the Coral Sea Basin and the Solomon Basin by the sill south of New Georgia. This water of high salinity can be followed further south of San Cristobal to Station 179, where a distinct salinity maximum of 34·718‰ appears at a potential temperature of 1·50° between depths of 3000 and 4500 m. Below 4500 m, as shown in Figure 6, salinity and potential temperature decrease towards the values of the central Pacific deep water. This shows that the water of comparatively high salinity in the Coral Sea and Solomon Basins leaves through the San Cristobal Trench, mixes with central Pacific deep water, and this mixture enters the New Hebrides Basin. The maximum salinity in the New Hebrides Basin is 34·700‰, which is higher than the value of 34·691‰ observed at Station 58.

The potential temperature in the basin is 1·48°C, and this temperature is found outside the basin at about 3400 m; it is therefore concluded that the sill depth of the ridge in 13° 30′ S., is approximately 3400 m. The potential temperature–salinity relation of Station 121, which is inside the New Hebrides Basin, shows a salinity of 34·711‰ at a potential temperature of 1·52°, indicating an overflow of water from the Coral Sea Basin over the ridge extending northwards from Chesterfield Reef.

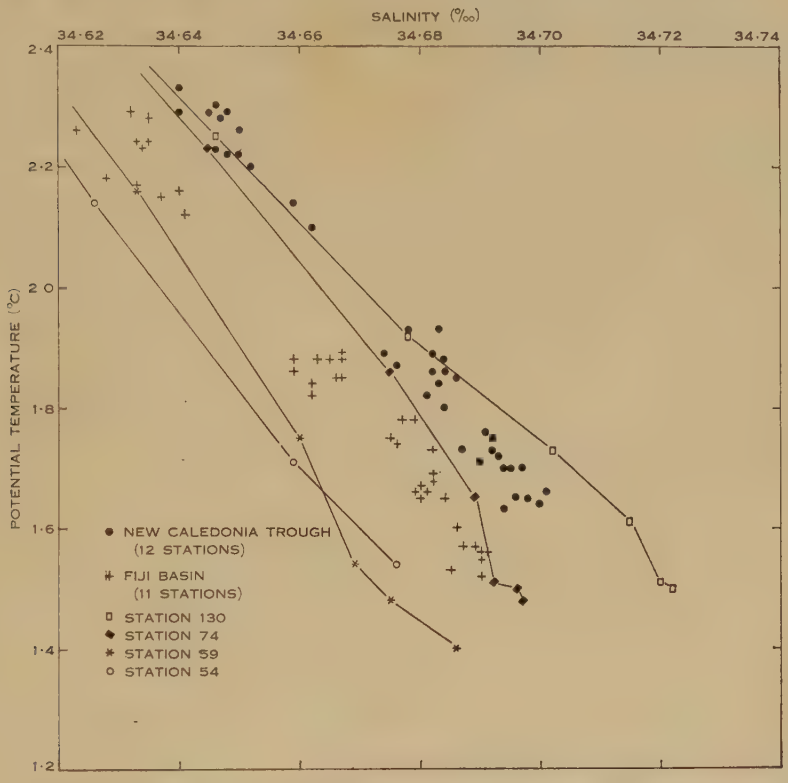


Fig. 7.—Potential temperature–salinity diagram for stations in the New Caledonia Trough and in the Fiji Basin. For position of individual stations see Figure 1.

The potential temperature–salinity relations of the water in the Fiji Basin and in the New Caledonia Trough (Fig. 7) are closely related to those of the New Hebrides Basin, represented by Station 74. The bottom water in the New Caledonia Trough has almost the same salinity values as the water in the New Hebrides Basin, but its potential temperatures are slightly higher because this basin is much shallower. The minimum potential temperature in the trough is 1·63°C, a value which is found outside the trough at 3000 m. The sill depth of the New Caledonia Trough, determined in this way, is consistent with the soundings. The potential temperature–salinity relation of Station 130 in the Coral Sea (Fig. 7) shows the influence of the water of high salinity from the Coral Sea on the salinity in the New Caledonia Trough. This influence is especially strong at potential temperatures above 1·80°C, that means above 2500 m.

The water in the New Caledonia Trough, influenced by water from the Coral Sea, has slightly higher salinities than that in the New Hebrides Basin; in contrast, the water in the Fiji Basin influenced by water from the central Pacific Basin, has lower salinities than that of the New Hebrides Basin. Figure 7 indicates that the water of the Fiji Basin is a mixture of water from the New Hebrides Basin, which is the major component, and water from the trough between Fiji and the New Hebrides. The potential temperature of the bottom water of the Fiji Basin is 1·52°C, and this value is found in the New Hebrides Basin at about 3400 m. Therefore the sill depth of the ridge closing the New Hebrides Basin must be of the order of 3400 m (Section II). On the other hand, the sill depth of the ridge connecting Fiji with New Hebrides is certainly not greater than 3000 m and the bottom to the north of this ridge is of similar depth, so the influence of water flowing over this ridge cannot be as strong as that entering over the deeper sill from the New Hebrides Basin. As a consequence, the water from the New Hebrides Basin forms the bottom water in the Fiji Basin and the water overflowing the ridge to the north affects only the higher levels. This influence can be recognized in Figure 7 by the lower salinity values at potential temperatures above 1·80°C, corresponding to depths of less than 2500 m.

Two smaller basins, the Norfolk Basin and the Havre Trough, are probably supplied from the Fiji Basin with water at depths of less than 3000 m, but as no stations were worked in these basins, data are not available.

## VII. The Flow of Bottom Water

From this analysis of the water masses, conclusions can be drawn about the flow of water filling the deep sea basins in this region and these movements have been indicated by arrows in Figure 1. In the East Australian Basin, Deep Water characterized by a salinity maximum spreads north at the 3000 m level. Part of this water overflows two sills of approximately 2850 m into the Coral Sea Basin forming its bottom water, which ascends slowly, thus becoming slightly heated and diluted by mixing with the water above it. This ascending water enters the Solomon Basin through a channel of about 3400 m sill depth. Part of this water forms the bottom water in the Bougainville–New Britain Trench, and part escapes over the sill south of New Georgia into the San Cristobal Trench, where it forms a salinity maximum between 3000 and 4500 m. Other water of high salinity seems to leave the Coral Sea Basin south of Rennell Island and probably north of Chesterfield Reef, but data on the bottom topography are too scanty to permit conclusion. Deep water from the central Pacific Ocean enters the Solomon Sea through the passage between Bougainville and New Ireland, but its effect is limited to depths between 2500 and 3000 m.

The deep water of the central Pacific Basin extends south into the deeper portions of the sea floor between the Solomons and the New Hebrides, and between New Hebrides and Fiji. In the vicinity of the San Cristobal Trench it mixes with the water of higher salinity escaping from the Solomon and Coral Sea Basins. This mixed water enters the New Hebrides Basin over a sill of about 3400 m depth, and forms its bottom water. From the New Hebrides Basin water flows at the 3000 m

level into the New Caledonia Trough and fills it to its southern end. Another part of the water in the New Hebrides Basin flows into the Fiji Basin over a sill approximately 3400 m. Other water enters the Fiji Basin directly from the north over the ridge running south-west from the Fiji Islands with a sill depth of only 3000 m.

In the General Bathymetric Chart of the Oceans (Sheet A'III) the deepest connection of the Solomon Basin and the Coral Sea Basin with the central Pacific Ocean is shown north and south of Rennell Island, thus indicating that both basins would have to be filled with water from the central Pacific. The most striking result of the analysis in this paper is the fact that both the Coral Sea Basin and the Solomon Basin are supplied with water from the East Australian Basin and not from the central Pacific Ocean. The topography, based on more comprehensive recent soundings (see Section II), also shows that these two basins are connected by a channel of at least 3400 m depth, and that the sill of the whole system is south of New Georgia, with a sill depth of about 3000 m. The sill connecting the Coral Sea Basin in the south with the East Australian Basin is only 2850 m deep. This is a case, probably unique and as yet unexplained, where the inflow into a basin is over the shallower, and the outflow over the deeper, of two sills. A pressure gradient from south to north causing a flow of water from the East Australian Basin towards the central Pacific Ocean may be advanced as the reason for this flow, but it is difficult, if not even impossible, to establish such a pressure gradient. However, some indication is given by a comparison of the densities in the two areas, in the 2850 m level corresponding to the sill depth of the Coral Sea Basin in the south. The density is $\sigma_t = 27{\cdot}80$ in the East Australian Basin, but in the central Pacific Ocean it is $\sigma_t = 27{\cdot}74$ (Stations 58 and 59). Such a density gradient in these depths is considerable and may be responsible for this unusual flow.

The properties of the bottom water in the different basins of the western South Pacific Ocean are given in Table 1.

## VIII. An Estimation of the Water Balance of the Coral Sea Basin

The vertical distribution of temperature in deep sea basins is characterized by an exponential decrease of potential temperature towards the bottom. The shape of this curve is determined by the conduction of heat penetrating into the basin from higher levels and by the ascending motion of the water inside the basin. We shall consider a basin which is continuously supplied by an inflow of water at the rate $Q$ (cm$^3$/sec). It can be assumed that this water sinks immediately to the bottom of the basin. This downward movement must be compensated for by ascending motion in the other parts of the basin. If $w(z)$ is the velocity of the ascending motion, and $F(z)$ the area of the basin in the depth $z$, the water balance is given by

$$Q = F(z)w(z).$$

The inflowing water may have the temperature $t_i$ so that a quantity of heat equal to $cQt_i$ enters the basin, where $c$ is the specific heat of water. The heat given off by the ascending water in the depth $z$ is then $cFwt$, and is greater than that of the inflowing water, because in all observed temperature distributions the potential temperature decreases down to the bottom. This upward flow of heat is, however,

TABLE 1

PROPERTIES OF THE WATER IN THE DEEP SEA BASINS OF THE WESTERN SOUTH PACIFIC OCEAN

| Name of Basin | Maximal Depth (m) | Sill Depth (m) | Observed Temperature Minimum | | | Minimum of Potential Temp.* (°C) | Bottom Water | | Remarks |
|---|---|---|---|---|---|---|---|---|---|
| | | | Depth (m) | Temp. (°C) | Potential Temp. (°C) | | Salinity (‰) | Oxygen (ml/l) | |
| East Australian Basin | 5941 | 3500 | 4250 | 1·15 | 0·80 | 0·79 | 34·735 | 4·23 | Off Sydney |
| | | | | | | (4400 m) | | −4·54 | |
| Coral Sea Basin | 4899 | 2850 | 3900 | 1·80 | 1·47 | 1·46 | 34·722 | 4·21 | Connected with Solomon |
| | | | | −1·84 | −1·51 | (4500 m) | −34·731 | −4·36 | Basin at 3400 m |
| Solomon Basin | 9140 | 3000 | 2800 | 1·87 | 1·67 | 1·63 | 34·710 | 3·43 | Connected with Coral Sea |
| | | | | −1·91 | −1·70 | (7750 m) | −34·713 | −3·73 | Basin at 3400 m |
| Central Pacific Basin | — | — | 3500 | 1·72 | 1·44 | 1·40 | 34·690 | 3·44 | As from Stations 58 and 59 |
| | | | | | | (4700 m) | | | |
| New Hebrides Basin | 7660 | 3400 | 3500 | 1·79 | 1·49 | 1·48 | 34·695 | 3·52 | |
| | | | −3700 | −1·81 | −1·52 | (4400 m) | −34·70 | −3·69 | |
| New Caledonia Trough | 4005 | 3000 | No temperature minimum | | | 1·63 | 34·694 | 3·57 | |
| | | | | | | (3450 m) | −34·701 | 3·69 | |
| Fiji Basin | 5931 | 3400 | 3700 | 1·85 | 1·55 | 1·52 | 34·690 | 3·52 | |
| | | | | | | (4000 m) | −34·691 | −3·66 | |

* As the observations do not reach to the bottom of the deepest depressions of the basins, the depth of the actual observed minimum of potential temperature is given.

opposed by a turbulent conduction of heat from higher levels into the basin, which transports a quantity of heat equal to $cFA\mathrm{d}t/\mathrm{d}z$ downwards, where $A$ is the coefficient of vertical eddy conductivity. The equation of the heat balance of the basin is therefore

$$Qt_i = Fwt - FA\mathrm{d}t/\mathrm{d}z.$$

For $t$ the potential temperature must be used, which is independent of vertical movements. If we introduce the relation $Q = Fw$, the equation

$$A\mathrm{d}t/\mathrm{d}z = w(t - t_i)$$

follows. If the vertical distribution of temperature is known, the value of the quotient $w/A$ can be calculated, because

$$w/A = \mathrm{d}[\ln(t - t_i)]/\mathrm{d}z.$$

To demonstrate this relation for the Coral Sea Basin, the logarithm of potential

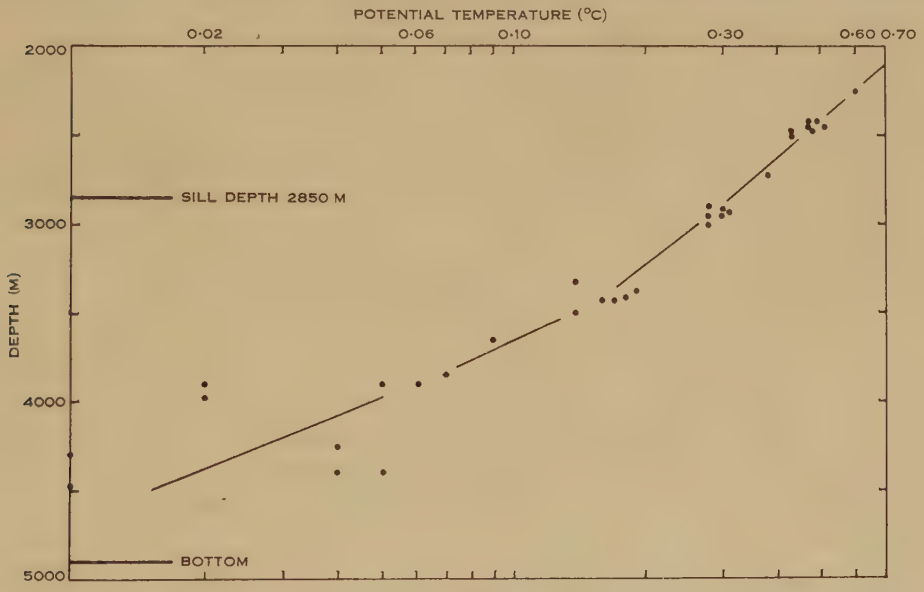


Fig. 8.—Potential temperature as a function of depth in the Coral Sea Basin. (Potential temperature shown on a logarithmic scale.)

temperature is plotted for seven stations against depth in Figure 8. For the temperature of the inflowing water the value $t_i = 1{\cdot}46$ has been taken, corresponding to the minimum of the observed potential temperature. Figure 8 shows that the slope of the function $\ln(t - t_i)$, and consequently the value of $w/A$, increases with increasing depth. If $A$ is considered constant inside the basin, $w$ must increase with depth, which is consistent with the fact that the area $F$ of the basin decreases.

Numerical values of $w/A$ and of $Q$ have been calculated for the depth intervals 3000–3500 m and 3500–4000 m. For the vertical eddy conductivity the value $A = 1$ has been assumed and the areas $F$ of the basin in 3250 and 3750 m depth were determined from the General Bathymetric Chart. The results of the calculation are shown in Table 2. The vertical upward velocities $w$ are of the same order

as those in the oceanic thermocline (Stommel 1958; Wyrtki 1961). Their variation with depth is due to the change of the area of the basin, which is confirmed by the constant value $Q$ for both levels. The rate of inflow into the basin is determined to $Q = 0{\cdot}045$ million $m^3$/sec, and is a very small value compared with ocean currents. Such an inflow could be effected by a current flowing at 2 cm/sec over a sill 20 km wide and having a vertical extension of 100 m. The vertical velocity indicates that the water would need about 100 years to ascend 500 m, provided $A = 1$.

TABLE 2

CALCULATION OF THE VERTICAL UPWARD VELOCITY $w$ AND OF THE RATE OF INFLOW $Q$ INTO THE CORAL SEA BASIN

| Depth | $t-t_i$ | $w/A$* | $w$(cm/sec) | $F$(cm$^2$) | $Q$(cm$^3$/sec) |
|---|---|---|---|---|---|
| 3000 | 0·27 | | | | |
| 3250 | | $1{\cdot}27\times10^{-5}$ | $1{\cdot}27\times10^{-5}$ | $35\times10^{14}$ | $4{\cdot}45\times10^{10}$ |
| 3500 | 0·14 | | | | |
| 3750 | | $1{\cdot}90\times10^{-5}$ | $1{\cdot}90\times10^{-5}$ | $24\times10^{14}$ | $4{\cdot}56\times10^{10}$ |
| 4000 | 0·05 | | | | |

* $w/A = \mathrm{d}[\ln(t-t_i)]/\mathrm{d}z$.

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# THE TASMANIAN TROUT FISHERY

## IV. THE RIVERS OF THE SOUTH AND SOUTH-EAST

By A. G. Nicholls*

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*Summary*

Two main river systems are included in this region, the Derwent and the Huon. Data derived from anglers' returns are analysed for each system separately but those from the Huon are insufficient for a thorough study. There is some doubt as to the representativeness of returns from either system. No significant changes have been found in the fishery over a period of 12 seasons either in the rate of daily catch per angler or in the length of fish taken. A study of the fish taken in an upstream trap at spawning time yields an annual mortality rate of about 60% for the Derwent River System and recaptures of tagged fish show a similar rate. Population estimates based on recaptures of tagged fish and on the spawning potential within the system indicate a total population of between one-half and one million, of which about 20% is of takable size. The contribution made by the release of hatchery-reared fish is shown to be insignificant. Evidence is produced which leads to the conclusion that there may be two distinct races of trout in Tasmania, the result of separate introductions of river and sea trout, distinguished by inherent meristic differences as well as by differences in growth rate and habits.

## I. Introduction

This paper, the fourth in the series dealing with the trout fishery in Tasmania, covers the rivers of the southern part of the State, corresponding with the Southern and South-East Regions as defined in the "Regional Planning Atlas" (Tasmania, Director of Industrial Development 1956) but includes a part of the Midland Region through which flow the upper stretches of the majority of the tributaries of the Derwent River, the most important river in the area. Several of these tributaries have their origin in lakes, most of which are now affected by the development of hydroelectric power. In addition, several new lakes have been constructed by the Hydro-Electric Commission in the courses of the tributary rivers, or as diversions. Much of the constructional work has been carried out since 1954, so that the present review of the fishery covers the period prior to modification brought about by hydro-electric development. A slight departure will be made from the earlier method of dealing with the data, most of which come from the Derwent River System. Very little information is available from the other rivers and a survey of the region would be greatly influenced by the results from the Derwent River. Each will be dealt with separately and no general review will be made of the region. For a general understanding of the treatment used here and for evaluating the statistical treatment, reference should be made to Part I (Nicholls 1957).

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## II. The Derwent River System

### (*a*) *Environmental Characteristics*

The Derwent River is over 100 miles in length from the point where it leaves Lake St. Clair to Bridgewater, at which point it is assumed to discharge into the estuary. Guiler (1955) has given an account of the hydrology of the River Derwent, his observations extending from the vicinity of the Port of Hobart to New Norfolk. The river is influenced by tides as far as New Norfolk, about 10 miles above Bridgewater, and the arbitrary point delimiting the tidal water fishery is fixed about midway between New Norfolk and Bridgewater, which is in the gradient zone (Guiler 1955). At Bridgewater the river is about three-fourths of a mile in width and below that point the estuary has the typical configuration of a drowned valley. Hobart is about 13 miles below Bridgewater and the estuary extends for about another 12 miles before opening gradually into Storm Bay.

From Lake St. Clair the river follows a generally south-easterly course to New Norfolk, from which point it runs north-easterly to Bridgewater, where it resumes its original direction. About 5 miles below Lake St. Clair it flows into Lake King William, a storage lake formed by the construction of the Clark Dam at Butler's Gorge about 7 miles downstream. At 15 miles below the dam it receives its first major tributary, the Nive River, which with its tributaries drains a large portion of the Central Plateau lying to the north. The Florentine River enters from the south, about 3 miles below the Nive. The Dee River, draining Lake Echo, the Ouse River, receiving water from the Great Lake via its tributary the Shannon River, and the Clyde River, draining Lakes Sorell and Crescent, enter from the north in that order during the next 20 miles. The Jordan River is the last major tributary from the north and enters the estuary just below Bridgewater. Between the Clyde and Jordan rivers there are three tributaries from the southern part of the basin, the Russell Falls River (recently renamed the Tyenna), the Styx, and the Plenty. There are numerous other minor tributaries joining the Derwent during its course, and many small creeks flow into the estuary before it reaches Storm Bay.

The total area of the Derwent River Basin is about 3700 sq. miles. More than one-half lies above the 2000-ft contour, and about one-quarter is above 3000 ft. The annual rainfall in the higher altitudes reaches 50–60 in. per annum, but much of the basin receives less than 30 in. The mean gradient of the main stream is about 20 ft per mile. River flow measurements at Macquarie Plains, about 15 river miles upstream from New Norfolk, show that the mean monthly flow from 1922 to 1948 was 5000 cu. ft/sec (range, 240 to 50,000) at which time the flow from the Great Lake via the Shannon and Ouse Rivers was under control. The closure of the Clark Dam in 1949 did not seriously affect these figures, the flow from 1950 to 1957 being 4360 cu. ft/sec (range, 900 to 61,000). During the latter period much of the water has come under control by the construction of water storages in the valleys of the Nive, Dee, and recently the main stream of the Derwent, so that the flow in the lower reaches is now subject to considerable control. The lower reaches of the main stream and its major tributaries lie in a region of intense cultivation occupying good agricultural land in one of the more densely populated areas of the State. There is a considerable fishery throughout its basin.

In the analysis which follows that section of the river which lies between Lake St. Clair and Lake King William is excluded from consideration since it is governed by lakes regulations in respect of times of fishing and size of fish. It will be dealt with in a later paper.

### (*b*) *Results and Discussion*

(i) *The Daily Catch.*—In Table 1 are given the results of the analysis of anglers' catches for the tidal and fresh waters of the Derwent River System separately for 8 seasons, and combined for 12 seasons. The numbers of anglers making returns varied from 7 to 38. Although from time to time reliable data were reported for individual rivers within the system, these were insufficient for adequate comparisons of the fishery between tributaries, and they have therefore all been included in the Derwent River System fishery in fresh waters.

TABLE 1

MEAN DAILY CATCH PER ANGLER FOR THE DERWENT RIVER SYSTEM

| Season | Tidal | | | Fresh | | | Combined | | |
|---|---|---|---|---|---|---|---|---|---|
| | No. of Fish | No. of Days | Fish/ Day | No. of Fish | No. of Days | Fish/ Day | No. of Fish | No. of Days | Fish/ Day |
| 1945–46 | — | — | — | — | — | — | 330 | 110 | 3·0 |
| 1946–47 | — | — | — | — | — | — | 286 | 76 | 3·8 |
| 1947–48 | — | — | — | — | — | — | 230 | 93 | 2·5 |
| 1948–49 | — | — | — | — | — | — | 41 | 20 | 2·1 |
| 1949–50 | 65 | 46 | 1·4 | 341 | 145 | 2·4 | 406 | 191 | 2·1 |
| 1950–51 | 100 | 77 | 1·3 | 277 | 122 | 2·3 | 377 | 199 | 1·9 |
| 1951–52 | 61 | 45 | 1·4 | 150 | 68 | 2·2 | 211 | 113 | 1·9 |
| 1952–53 | 89 | 58 | 1·5 | 116 | 48 | 2·4 | 205 | 106 | 1·9 |
| 1953–54 | 71 | 51 | 1·4 | 35 | 18 | 1·9 | 106 | 69 | 1·5 |
| 1954–55 | 8 | 6 | 1·3 | 60 | 35 | 1·7 | 68 | 41 | 1·7 |
| 1955–56 | 25 | 19 | 1·3 | 136 | 70 | 1·9 | 161 | 89 | 1·8 |
| 1956–57 | 15 | 13 | 1·2 | 613 | 245 | 2·5 | 628 | 258 | 2·4 |
| 1945–1957 | 434 | 315 | 1·38 | 1728 | 751 | 2·30 | 3049 | 1365 | 2·23 |

In tidal waters the daily catch has remained close to the average of 1·4 fish per angler per day. The overall trend has been slightly upwards but statistical analysis shows that the variation between the means for each season is of the magnitude of the sampling error only, indicating no significant change in the fishery. In fresh waters the seasonal means for daily catch show some fluctuation, with an overall downward trend; but again statistical analysis shows no significant difference between the means. The combined figures for 12 seasons show a downward trend which is statistically quite significant. It was suggested in an earlier paper (Nicholls 1958*b*) that the change in the nature of the returns sought from anglers for 1949–50 onwards might have had some influence on the results, and it was shown that although the mean catch for the first four seasons was higher than that for later seasons, there

was no significant difference within each group. The same results appear here, and while the mean daily catch per angler up to 1948–49 was 2·97 fish, which fell to 2·03 fish for the next eight seasons, within each group the differences were not significant. It will be noted that although the mean daily catch for all seasons fell somewhat in 1953–54, it was followed by a progressive recovery, and these changes may be regarded as due to normal seasonal fluctuations. The value for 1956–57 shows a rise to 2·4 fish per day, but this result was due to a good series of returns from the Bothwell district, covering fishing in the Clyde, Little Pine, Nive, Shannon, and Ouse Rivers. Of the 19 returns recording fishing in the Derwent River System, 15 were from this centre, and the mean daily catch for these was 2·5, while that for the remaining five was 0·75.

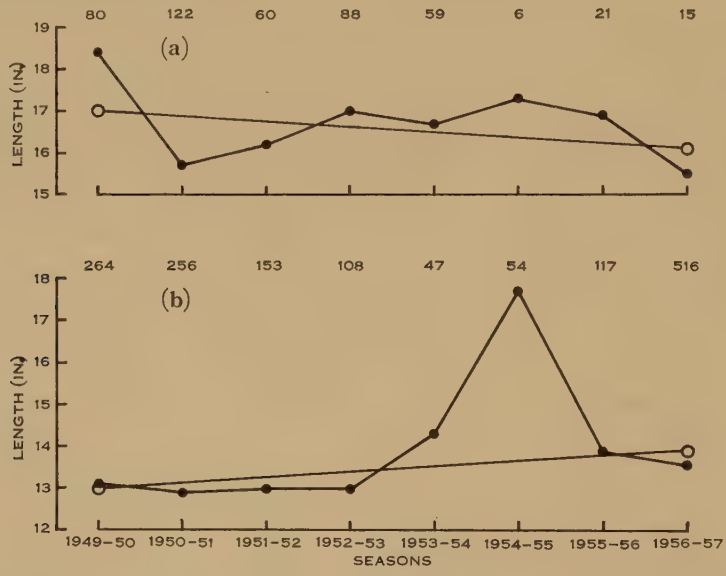


Fig. 1.—Mean lengths of fish from the Derwent River System from 1949–50 to 1956–57: (*a*) in tidal waters; (*b*) in fresh waters. The numbers of fish measured in each season are given above each graph.

(ii) *Fish Lengths.*—During the first five seasons, 409 fish lengths from tidal waters were recorded by anglers, and 828 from fresh waters in the system. In the next three seasons 42 were recorded from tidal waters and 687 from fresh waters. The first five seasons are those for which results were given in the earlier papers of this series. Statistical analysis shows differences between the means to be quite significant for the eight seasons in tidal waters; in fresh waters they are not significant for five seasons, but quite significant for eight seasons. Although in tidal waters the differences are significant there is no steady trend and they may be regarded as sampling fluctuations due to the relatively small samples over a size range of from 12 to 30 in. In fresh waters there was a marked increase in the later years. It is possible that this also may be due to inadequate sampling, since the size range is even greater (9–32 in.) and it is very doubtful if samples of less than 100 are representative. The values are plotted in Figure 1, and the regression lines indicate the overall trends. The higher than normal values in 1953–54 in fresh waters were due to the inclusion of a large

proportion of fish measurements from the lower Derwent, and the absence of records from the tributaries. Means for 1955–56 and 1956–57 were somewhat affected by the inclusion of small numbers of large fish from the Little Pine River above the recently formed lagoon. Analysis for different sources where sufficient data were available shows that in the Ouse River and its tributaries, 385 fish measured during seven seasons averaged 13·3 in., and in the Clyde River, 469 fish measured during seven seasons averaged 13·7 in. An average for the Derwent itself during seven seasons was 14·6 in. based on 317 measurements. Variation between seasons within each source was statistically significant.

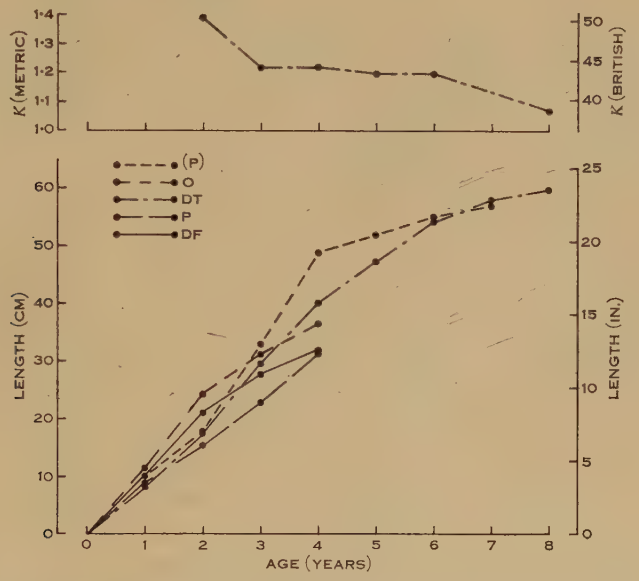


Fig. 2.—Mean lengths-for-age of fish from various sources in the Derwent River System, and condition ($K$) for fish from tidal waters. DF, Derwent River, fresh; DT, Derwent tidal waters; O, Ouse River; P, Plenty River; (P), one fish from the Plenty River not included in the pooled means.

(iii) *Growth and Age.*—Comparatively few scale samples from fish from these rivers are available from anglers' collections. In 1949–50, 22 samples were taken from fish in tidal waters, and 31 from fresh waters; in the following season there were 32 from tidal, and 52 from fresh. The majority of the latter came from a good collection made by one angler. The results of studying these scales are shown in Figure 2. In tidal waters, from which two 2-year fish were excluded, there was no statistically significant difference within age groups between the two seasons and the data have been pooled. Three sources were represented in fresh waters, the Derwent River between Hayes and Plenty in 1949–50 (16 fish), the Plenty River (1949–50, 14 fish; 1950–51, 3 fish), and the Ouse River (1950–51, 49 fish); the few fish from the Plenty River in both seasons have been pooled.

Figure 2 shows a different growth rate at each of the three sources in fresh water, up to 4 years of age; statistically the differences are significant at the 1% level at $L_1$; very highly so at $L_2$, somewhat less so at $L_3$, and not significantly

TABLE 2

TAGGED AND MARKED FISH RELEASED IN THE DERWENT RIVER SYSTEM

| Date | Tag No. or Fin Clip* | No. of Trout† | Kind of Trout | Age | Source | Place of Release | No. Recaptured |
|---|---|---|---|---|---|---|---|
| June 1949 | L.102–140 | 35 | Brown | var. | Plenty Hatchery | Plenty River | 2 |
| Oct. 1949 | L.1–49 | 45 | Rainbow | ? | Great Lake | Ouse River (Skittleball Plains) | 7 |
| Sep. 1950 | M.3803–3814 | 12 | Brown and rainbow | 2+ | Plenty Hatchery | Plenty River | 1 |
| Sep. 1950 | L.428–435 | 8 | Brown | var. | Derwent Estuary (Lowestoft Bay) | At source | 0 |
| Apr.–June 1951 | M.4101–4207 | 104 | Brown | var. | Plenty River (Fish Trap) | Plenty River | 24 |
| Sep. 1951 | S.635–638 | 101 | Brown | 1+ | Plenty Hatchery | Derwent River (Dry Creek) | 0 |
| | *lV* | 4900 | Brown | 1+ | | | 5 |
| Oct. 1951 | S.946–1076 | 98 | Brown | 2+ | Plenty River | Plenty River | 0 |
| | *r & lV* | 157 | Brown | 2+ | Plenty River | Plenty River | 0 |
| Nov. 1951 | *rV* | 1000 | Brown | 1+ | Miena Hatchery | Clyde River (Bothwell) | 0 |
| | *lP* | 1300 | Brown | 1+ | Miena Hatchery | Dee River (Lyell H'way) | 0 |
| Mar. 1952 | S.2001–2149 | 142 | Rainbow | 2+ | Plenty Hatchery | Derwent River at mouth of Plenty | 13 |
| | S.2150–2268 | 119 | Brown | | | | 6 |
| Sep. 1952 | S.2781–2820 | 39 | Brown | var. | Plenty River and Hatchery | Plenty River | 2 |
| | *rP* | 4800 | Brown | 1+ | Plenty Hatchery | Clyde River (Bothwell) | 0 |
| | *r & lP* | 32 | Brown | 2+ | Miena Hatchery | Derwent River (Dry Creek) | 0 |
| | | 116 | Rainbow | | | | |
| | *lP & rV* | 5100 | Brown | 1+ | Plenty Hatchery | Ouse River, Ouse | 0 |
| | *rP & lV* | 199 | Rainbow | 2 | Plenty Hatchery | Derwent River (Dry Creek) | 1 |
| May 1953 | M.3902–3920 | 9 | Brown | 5 | Plenty Hatchery | Plenty River | 2 |
| June–July 1953 | M.4397–4521 | 108 | Brown | ? | Great Lake | Plenty River | 19 |

* Tag numbers are preceded by S., small; M., medium; or L., large, indicating size. *r* or *l* indicate right or left; *V* or *P* indicate ventral or pectoral fins.

† These may be fewer than the number apparently tagged because of missing or damaged tags. Occasionally, also, fish died before release.

different at $L_4$. This suggests that there are real differences in growth rate at each source which becomes less marked as the fish age because of the inclusion in the catches of some fish which have visited the estuary after their second or third year but were residing upstream at time of capture (Nicholls 1958*a*). Support for this is given by the growth of all fish taken in tidal waters in these seasons, shown in Figure 2. In the early years these fish had a growth rate intermediate between the best and poorest of fish from freshwater sources, but it rose to above the best at the fourth year and continued at a higher level. The growth of one 7-year fish taken in the Plenty River appears exceptional in its third and fourth years which, it is reasonable to assume, were spent in tidal waters.

(iv) *Condition.*—The mean values for fish from tidal waters of the Derwent, pooled for two seasons, are shown in Figure 2. It is doubtful if the figures have much value because of the small amount of data involved, and the variability within samples due to the weighings having been made by several anglers. They show the general trend of decrease in value with increase in age, and mean values suggest that the Ouse River (43·4) grows better-conditioned fish than the Plenty (38·9) which in turn is better than the main river (30·0). The condition in tidal waters (43·4) is also good.

(v) *Tagged and Marked Fish.*—Table 2 shows the details of liberations and recoveries of tagged and marked fish for the Derwent River System. Of the fish recorded in this table those released in October 1949 and July 1953 were from the Great Lake and relate to that fishery; discussion of these will be deferred to the appropriate paper. Of the remainder only the 1951 upstream migrants taken in the fish trap yielded much information.

During this spawning run in the Plenty River (April to June 1951) 104 fish were tagged, and 24 of these have since been recaptured, some more than once; the data relating to these are given in Table 3. Eight of these fish were taken by anglers during the 1951–52 season, and most of these had moved downstream. Two had reached tidal waters in the vicinity of Bridgewater, 18 miles by water from the point of release after tagging; one had travelled only 8 miles, and another about 10 miles downstream; three taken late in the season were caught in the Plenty River near its junction with the Derwent and it is almost certain that they were returning to their spawning grounds in the Plenty River. In fact, another ten tagged fish were taken in the trap during the next month. The only exception to the downstream migration was a fish reported at third hand to have been taken in November in an irrigation channel on the Lawrenny Estate, about 25 miles up the main stream of the Derwent River, which, if the report is reliable, represents a most remarkable migration for a fish which had just finished spawning.

Of the ten fish which returned to the Plenty River to spawn in 1952, two returned to the same river in 1953, and none of the other eight has been reported as having been taken by anglers. Of these two fish, one has not been seen again, but the other returned to the same place in both 1954 and 1955. In addition, one of the sample tagged in 1951 was not seen again until 1953, and a second not until 1954, when they were trapped in the Plenty River. There remain four fish which survived the first season and were not recorded as having passed up the Plenty River in 1952;

of these one was taken at New Norfolk and one at Bridgewater in September 1952, and two were taken from the Derwent close to the mouth of the Plenty River in the early part of the 1953–54 season.

TABLE 3

RECORD OF RECAPTURES OF FISH TAGGED IN THE 1951 SPAWNING RUN

| Tag No. | Fish at Tagging | | Length (in.) at Spawning Run | | | | Fish Taken by Anglers | | |
|---|---|---|---|---|---|---|---|---|---|
| | Length (in.) | Age (Years) | 1952 | 1953 | 1954 | 1955 | Date | Length (in.) | Place |
| 4103 | 20·4 | 5 | | | | | 16. ix.51 | 21·5 | Old Lime Kiln |
| 4108 | 18·1 | 4 | 19·5 | | | | | | |
| 4115 | 17·0 | 5 | 18·0 | | | | | | |
| 4117* | 17·8 | 4 | | | | | 13. x.51 | ?18·0 | Bridgewater |
| 4119 | 16·5 | 5 | | | | | 21. ix.52 | 18·7 | Bridgewater |
| 4120† | 17·1 | ? | 17·7 | | | | | | |
| 4122 | 17·4 | 5 | | | | | 28. iv.52 | 20·0 | Plenty R. mouth |
| 4124 | 16·5 | 4 | 17·4 | | | | | | |
| 4127 | 14·0 | 5 | | | | | 15. x.51 | 15·0 | New Norfolk |
| 4130 | 19·1 | 5 | | | 22·0 | | | | |
| 4134 | 20·3 | 4 | | | | | 3. iii.52 | 21·5 | Plenty R. mouth |
| 4137 | 20·7 | 5 | | | | | 9. iv.52 | 21·5 | Plenty R. mouth |
| 4149‡ | 21·6 | ? | | no data | | | | | |
| 4151 | 18·8 | 6 | 19·9 | 20·7 | 21·3 | 21·8 | | | |
| 4152 | 17·9 | 4 | 20·9 | | | | | | |
| 4161 | 12·2 | 4 | | | | | 18. x.53 | 14·8 | Hayes |
| 4163 | 11·7 | 4 | | | | | 9. xi.53 | 12·5 | Derwent R., Plenty |
| 4168 | 15·6 | 5 | | | | | 19. xi.51 | ? | Lawrenny, Ouse |
| 4170 | 16·8 | 5 | 18·5 | | | | | | |
| 4173 | 13·3 | 3 | 15·4 | 17·2 | | | | | |
| 4192 | 10·9 | 3 | | | | | 13. ix.52 | 13·0 | New Norfolk |
| 4196§ | 17·2 | 4 | | | | | 22.viii.51 | ? | Bridgewater |
| ? | 20·5 | 5 | 21·3‖ | | | | | | |
| ? | 19·3 | 5 | 20·3‖ | | | | | | |

* Scales from 4117 at recapture showed good growth subsequent to spawning, suggesting that this fish was really about 19 in.

† Scales taken from 4120 at tagging were all replacements; none were taken from this fish in 1952.

‡ Scales from 4149 in 1951 were badly eroded and unreadable; only the tag was found in 1953, having become detached from the fish while it was being handled, so that no data are available.

§ It is known that tag No. 4196 was retained by the angler and no data were sent in.

‖ These two fish had recently lost their tags.

The evidence presented by the 12 fish taken by anglers seems to indicate that following the spawning run in the Plenty River fish migrate downstream to tidal

waters, at least as far as Bridgewater. There is also evidence that some at least of the fish found in the Plenty River at spawning time return there to spawn in subsequent years. One fish did so in five successive seasons.

There remains for consideration the balance of the 104 fish tagged in 1951, for 80 of which there is no further record. These tagged fish ranged from 3 to 6 years of age (12, 38, 43, and 7% respectively), and one of them survived to complete 10 years of life (No. 4151). Of the 104 fish tagged, eight were taken by anglers in the first season, providing a 7·7% mortality rate due to angling. It may have been somewhat higher as a result of anglers retaining tags and omitting to report their capture, known to have happened in only one case (4196). A study of the spawning run in the Plenty River (Section II(*c*)(v)) yields a value of about 60% per annum total mortality over age groups 4–10, and if this occurred between the spawning runs of 1951 and 1952, about 42 tagged fish should have survived that period. If the mortality due to angling was the same in the next season, then three of these fish should have been taken—two were reported. By the next season only 17 tagged fish might have been expected to survive, of which one should have been taken by anglers—again two were reported. In the two following seasons seven and three tagged fish were likely to have survived; two and one were known to have done so. None should have been taken by anglers, and none has been reported either by anglers or in subsequent spawning runs. These figures appear to confirm that the total annual mortality rate for fish over 3 years of age is about 60%, and that of this mortality about 8% is due to angling. The fate of the balance of the fish is unknown. Of the original 104, the fate of only 24 is known; of the 42, 17, 7, and 3 assumed to have survived until 1952, 1953, 1954, and 1955 respectively, only 16, 6, 2, and 1 can be accounted for, or approximately one-third of the probable survivors. It may be that the remaining two-thirds ran up streams other than the Plenty River in subsequent years. Unfortunately there is no evidence to support this, owing to the absence of trapping sites in other streams. It is also possible that they spawned in that river, but below the trap. Evidence is available that all fish originally tagged did not necessarily return to the trap each year since two fish (4149 and 4130) were not seen again until 1953 and 1954 respectively. During the spawning runs the river is liable to flood and swamp the trap, so that although under such conditions fish probably tend to take cover, some might have been in the trap when a flood occurred and escaped upstream before it receded. The trap was flooded late in June 1952, by which time most of the fish had run, but there were gaps of several days on three occasions in May and three in June, on which no fish were taken from the trap.

A total of 820 tagged fish was released in this System, of which 9·3% was recovered, 7·1% taken by anglers. An analysis by age at release shows that of 101 fish tagged as yearlings, none was recovered; of 371 fish tagged as 2-year fish, 5·4% was recovered (5·1% by anglers), and of 348 older fish, 16·1% was recovered (11·9% by anglers). Of the 17,600 marked fish released, mostly yearlings, only six were reported of which one was taken by an angler. The majority of all fish recovered was taken soon after liberation, close to the point of release.

(vi) *Mortality Rates.*—Because the number of scale samples available for study was so small, and because of the different growth rates in different parts of the

System disclosed by the scales, it is considered that any attempt to distribute the lengths of all fish taken by anglers might lead to invalid results. No attempt to estimate mortality from anglers' data will be made, but data are available from the spawning runs in the Plenty River which will be dealt with below (Section II(*c*)(v)).

(vii) *Annual Catch per Angler.*—This is based on all returns which record fishing in this System. The results of the analysis are given in Table 4. The figures for tidal waters show some variation around the mean for eight seasons; the differences are not statistically significant. In fresh waters, again for eight seasons, there

TABLE 4

MEAN ANNUAL CATCH PER ANGLER

| Season | Tidal | | | Fresh | | | Combined | | |
|---|---|---|---|---|---|---|---|---|---|
| | No. of Anglers | No. of Fish | Fish/ Angler | No. of Anglers | No. of Fish | Fish/ Angler | No. of Anglers | No. of Fish | Fish/ Anglers |
| 1945–46 | — | — | — | — | — | — | 7 | 330 | 47·1 |
| 1946–47 | — | — | — | — | — | — | 10 | 391 | 39·1 |
| 1947–48 | — | — | — | — | — | — | 17 | 302 | 17·8 |
| 1948–49 | — | — | — | — | — | — | 8 | 47 | 5·9 |
| 1949–50 | 13 | 64 | 4·9 | 20 | 316 | 15·8 | 30 | 380 | 12·7 |
| 1950–51 | 24 | 123 | 5·1 | 28 | 379 | 13·5 | 44 | 502 | 11·4 |
| 1951–52 | 13 | 61 | 4·7 | 15 | 181 | 12·1 | 27 | 242 | 9·0 |
| 1952–53 | 10 | 75 | 7·5 | 12 | 71 | 5·9 | 21 | 146 | 7·0 |
| 1953–54 | 6 | 32 | 5·3 | 9 | 42 | 4·7 | 14 | 74 | 3·3 |
| 1954–55 | 3 | 8 | 2·7 | 6 | 60 | 10·0 | 8 | 68 | 8·5 |
| 1955–56 | 8 | 25 | 3·1 | 12 | 136 | 11·3 | 17 | 161 | 9·5 |
| 1956–57 | 5 | 15 | 3·0 | 16 | 613 | 38·3 | 19 | 628 | 33·1 |
| 1945–46 to 1956–57 | 82 | 403 | 4·9 | 118 | 1798 | 15·2 | 222 | 3271 | 14·7 |

is considerable variation about the mean of 15·2, and the differences are statistically significant at the 1% level. When 12 seasons are compared, by combining the tidal and fresh water data, a considerable fluctuation is shown, with much higher values in the early years followed by a downward trend and some recovery, approaching those of earlier years during the final season. The differences between the seasonal means are not statistically significant, but this is entirely due to the remarkable apparent recovery during 1956–57; without the figures for this season the differences are statistically quite significant. This high value is due to the good series of returns received from one district, which really show what the average angler catches. It is not considered that there has been any real fall in the average catch per angler during the preceding six or seven seasons, but that the absence of adequate returns influenced the results unfavourably to give rise to the impression that there had been a decline.

TABLE 5

ESTIMATED TOTAL CATCHES FROM THE DERWENT RIVER SYSTEM

| Season | No. of Returns | No. Used in System | No. of Licences* | Estimated No. Fishing in System | Catch/ Angler | Estimated Total Catch | Coefficient of Variation | Standard Error† |
|---|---|---|---|---|---|---|---|---|
| 1945–46 | 18 | 7 | 874 | 340 | 47·1 | 16000 | 0·642 | 10000 |
| 1946–47 | 18 | 10 | 966 | 537 | 9·1 | 21000 | 0·557 | 11500 |
| 1947–48 | 28 | 17 | 1121 | 681 | 17·8 | 12100 | 0·311 | 3700 |
| 1948–49 | 11 | 8 | 1306 | 950 | 5·9 | 5600 | 0·463 | 2600 |
| 1949–50 | 49 | 30 | 1404 | 860 | 12·7 | 11000 | 0·288 | 3200 |
| 1950–51 | 57 | 44 | 1718 | 1326 | 11·4 | 15000 | 0·366 | 5500 |
| 1951–52 | 35 | 27 | 1901 | 1466 | 9·0 | 13000 | 0·293 | 3800 |
| 1952–53 | 35 | 21 | 2045 | 1227 | 7·0 | 8600 | 0·449 | 3900 |
| 1953–54 | 19 | 14 | 2186 | 1611 | 5·3 | 8500 | 0·454 | 3900 |
| 1954–55 | 16 | 8 | 2502 | 1251 | 8·5 | 10500 | 0·563 | 5900 |
| 1955–56 | 37 | 17 | 3110 | 1429 | 9·5 | 13500 | 0·340 | 4600 |
| 1956–57 | 26 | 19 | 4007 | 2928 | 33·1 | 97000 | 0·347 | 33500 |

* Excluding daily and weekly licences.

† Values over 10,000 adjusted to nearest 500, below to nearest 100.

(viii) *Estimated Total Catch.*—Figures for the estimated total catch from this river system are given in Table 5. These are based on the mean catch per angler and the numbers of returns which relate to fishing in this System. Two sources of variation are taken into account in computing the coefficient of variation and standard errors of the estimates (Nicholls 1958*b*). The figures show that in spite of the increase in the number of licensed anglers there has been a distinct downward trend in the estimated total catches, with some recovery towards the middle of the period and a marked recovery towards the end, particularly in the final season. There is some evidence to suggest that of recent years a greater proportion of anglers has been diverted to the newly constructed lakes, most of which are readily accessible to anglers of the southern region. This is best shown in a comparison of the numbers of

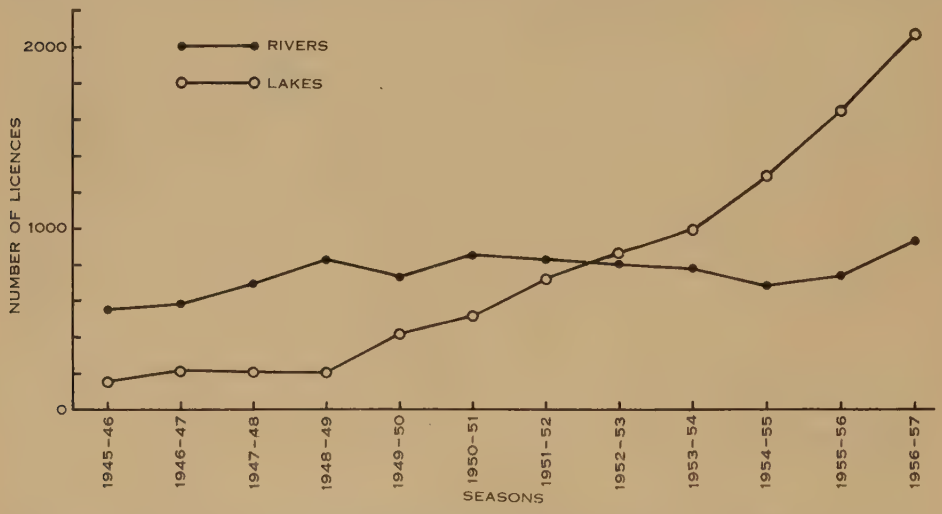


Fig. 3.—Numbers of seasonal licences issued to adult males in the Southern Region from 1945–46 to 1956–57.

licences issued for lakes and rivers fishing (Fig. 3). This comparison is based on the number of seasonal licences issued to adult males only, because during the period there were several changes in the type of licence issued to other classes of anglers.

It is clear that during the first four seasons the increase in total licences issued was among the river licences, but in 1949–50 there was a fall in the numbers of river licences and an increase in the number of lake licences; thereafter while the river licences have remained more or less constant, the number of lake licences has risen steadily in this district. The possession of a lake licence does not, of course, preclude river fishing and it is certain that many holders of lake licences also fish in rivers, but there has undoubtedly been a swing towards lake fishing and this, to some extent, has probably accounted for the fall in estimated total catch from this System. At the same time the question of true representation of the fishery by those who have made returns remains, illustrated by the fact that the increase in the total catch shown for 1955–56 and the very high figure for 1956–57 can both be related to the concerted effort made by a group of anglers in the Bothwell district during these two

seasons to ensure returns from a genuine cross section of anglers from that district. Their individual catches show figures similar to those at the beginning of the period, and there is no reason to doubt that such figures have persisted throughout the period but have not been disclosed. It is probable that there has been a steady increase over the period in conformity with the increase in the total number of licences issued.

Good catches are not uncommon in other parts of the Derwent from anglers who do not make returns. The results for one season's fishing from an angler who fished regularly in the lower reaches of the Derwent above tidal waters showed 51 days fishing for 147 fish, with a total weight of 284½ lb or 2·9 fish per day with an average weight of 1·935 lb. In another case, from the lower reaches of the Ouse River, one angler took 71 fish on 37 days, or 1·9 fish per day in one season, and 84 fish on 44 days or 1·9 fish per day in the following season; the average weight of these fish for each season was 1·34 and 1·31 lb. Such returns leave little doubt that the fish are there, and can be taken by the consistent angler who seldom makes returns unless specially asked to.

(ix) *Summary.*—In neither tidal nor fresh waters was there any significant difference in the mean daily rate of catch from 1949–50 to 1956–57. Over the longer period of 12 seasons, for which it is not possible to separate the tidal and fresh water fisheries, the difference is significant, but the downward trend of the middle years gave place to an upward trend during later years. Though there was some variation in the lengths of fish, this has been due to variation in the source of the data, and there has been no trend which could indicate any major changes in the fish population. The growth rate and condition of the fish have been normal. Relatively few of the tagged or marked fish released into the System have been recovered by anglers. Tagged fish showed a better recovery rate than marked fish, as is to be expected since a fin-clipped fish is more likely to be overlooked. The 9·3% recovery of tagged fish is relatively high, but it should be noted that all the fish recovered were at least 2 years of age at release. Marked yearlings have shown a very low rate of recovery, which rose to only 5% for 2-year fish. Figures suggest a mean annual catch of about five fish per angler from tidal waters and about 15 from inland waters but these are considered to be too low. Estimated total catches based on the mean catch per angler in relation to the number of licences issued in the southern region indicate a mean value of about 15,000 fish per annum for the Derwent River System over the past 12 seasons. Evidence is available which suggests that this figure is too low and that an estimate of about 20,000 fish would be nearer the correct figure. The total catch has probably risen steadily from about 5000 in 1945–46 to about 45,000 in 1956–57.

### (c) *The Spawning Run in the Plenty River*

(i) *Introduction.*—The Plenty River, though one of the minor tributaries of the Derwent, is important as the source of much information regarding the reproductive potential of the System. It is relatively short, not much over 30 miles in length, with numerous tributary creeks, most of which are probably of a temporary nature. It rises at an altitude of about 2000 ft and since the Derwent is little above sea level at the mouth of the Plenty, its average gradient is about 70 ft per mile. Much of the bed is composed of good spawning gravel with numerous pools over a hard bottom.

Though a normal shallow stream in summer, it is subject to quick rises after heavy rainfall in its headwaters when the level rises by several feet and the lower reaches are subject to occasional flooding. There are small falls in its course, and one of these, about 8 ft in height, occurs just below the hatchery.

It had been observed that upstream migrants had some difficulty in negotiating this fall, as a result of which a fish pass, incorporating a trap, was constructed early in 1950. During the spawning run of that season over 500 fish were trapped, and 80,000 eggs were obtained from mature fish, but no data were collected regarding the fish. Most of the fish run in May and June, although the run may begin in April and

TABLE 6

PLENTY RIVER SPAWNING RUNS

The summer runs are in *italics*

| Season | Dates | No. of Males | No. of Females | Totals | No. of Ova Stripped |
|---|---|---|---|---|---|
| 1951 | 29.iv–15.vi | 65 | 102 | 167 | 75,000 |
| 1952 | 20.iv–28.vi | 282 | 283 | 565 | 50,000 |
| 1953 | 24.iv–27.vii | 138 | 234 | 372 | 50,000 |
| 1954 | 15.iii–26.vi | 292 | 309 | 601 | 75,000 |
| 1955 | 2.iv–15.vii | 381 | 646 | 1027 | 150,000 |
| *1955–56* | *9.xii–24.ii* | *31* | *201* | *251* | — |
| 1956 | 12.iv–25.vii | 238 | 394 | 632 | 105,500 |
| *1956–57* | *21.xi–19.i* | *50* | *48* | *98* | — |
| 1957 | 19.iv–30.vii | 460 | 611 | 1071 | 220,000 |
| *1957–58* | *27.xii–21.ii* | *41* | *19* | *62* | — |
| 1958 | 31.iii–8.vi | 272 | 399 | 671 | 46,000 |
| 1959 | 7.iv–10.vii | 197 | 250 | 447 | — |

last through July. In 1951, by the end of June, about 300 fish had been handled. Of these, 167 were studied and 126 were tagged. From 1952 onwards, efforts have been made to trap every ascending fish. During floods, when the trap and surrounding country are under water, it is impracticable to collect fish and some may pass through undetected. Such floods, usually of short duration, are likely to occur on at least two or three occasions each season.

Normal winter runs of fish have occurred with regularity, but from December 1955 to February 1956 there first occurred an unexpected summer run of fish. These were not spawning fish, and examination of a sample showed that their gonads were in the condition expected at that time of year. This summer run has occurred in each of the two following seasons. In 1956–57 it started in November and continued into January, but in the most recent season (1957–58) it started in December and continued intermittently thereafter so that it has been difficult to separate it from the normal winter run. The hatchery superintendent states that the trap has been watched with sufficient care for him to be able to assert that there were no summer runs before 1955–56. The possible significance of this run will be discussed below.

(ii) *Composition of the Runs.*—This is best shown in tabular form, and the data are set out in Table 6. The normal winter runs have fluctuated somewhat in numbers, but the average (excluding 1951 which was incomplete) has been about 700 fish. In general, females have been more abundant than males, comprising about 58% of the runs. Table 6 also shows the number of ova stripped from these fish each season, which varies considerably according to the time during the run at which the majority of fish were trapped.

TABLE 7

NUMBERS OF FISH IN EACH AGE-GROUP IN SPAWNING RUNS

| Season | Age (Years) | | | | | | | | | | Totals |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | |
| 1952 | — | 30 | 174 | 127 | 107 | 26 | 7 | 3 | — | 1 | 475 |
| 1953 | 3 | 22 | 136 | 116 | 30 | 5 | 1 | 3 | 1 | 1 | 318 |
| 1954 | — | 18 | 124 | 204 | 98 | 36 | 6 | 6 | 2 | 2 | 496 |
| 1955 | — | 187 | 348 | 223 | 122 | 35 | 8 | 4 | 1 | — | 928 |
| 1956 | 1 | 86 | 257 | 122 | 49 | 22 | 4 | 1 | — | — | 542 |
| 1952–1956 | 4 | 343 | 1039 | 792 | 406 | 124 | 26 | 17 | 4 | 4 | 2759 |
| 1955–56* | 28 | 135 | 39 | 19 | 9 | — | 1 | 1 | — | 1 | 234 |

* Summer run.

From scale samples taken during the first six winter runs and the first summer run, it has been possible to allocate the fish to their age groups, and thus to study the composition of the runs with respect to age. The data are set out in Table 7; data for the 1951 winter run are omitted since only the tagged fish, which formed a part of the total run, were sampled. A considerable number of scales taken in each season were replacements and were rejected. The table shows that in each season the bulk of the spawners are 4- or 5-year fish, together constituting 60–80% of the total run; the lowest figure occurred in 1955 when there was an unusually large incursion of 3-year fish. The average for the five winter runs was 66%.

(iii) *Length, Weight, and Condition Factor.*—The mean lengths, weights, and $K$ values for each sex are plotted in Figure 4, for each run from 1952 to 1959, including the summer runs. In general the sexes were similar except that the females had a consistently higher $K$ value, as was to be expected with mature fish approaching spawning. The unusually high values for length and weight in 1954 coincided with the lowest proportion of 3- and 4-year fish in the runs (Table 7), and the fall which followed was due to higher proportions of fish of these ages. No scale samples were taken in later years but from Figure 4 it may be assumed that similar proportions were maintained in 1957 and 1958 with an increasing proportion of older fish in 1959.

(iv) *Growth Rates.*—The mean lengths for age of fish in all runs where scale samples were taken are plotted in Figure 5. During their first three years the fish of the summer run in 1955–56 were distinctly smaller than fish of the same ages from the normal winter runs: at these ages the differences are statistically quite significant. Thereafter the differences are not significant. In their fourth year they showed a sudden increase in length, overtaking the fish of the winter runs, and although the difference in mean length at $L_4$ is not statistically significant it is biologically quite

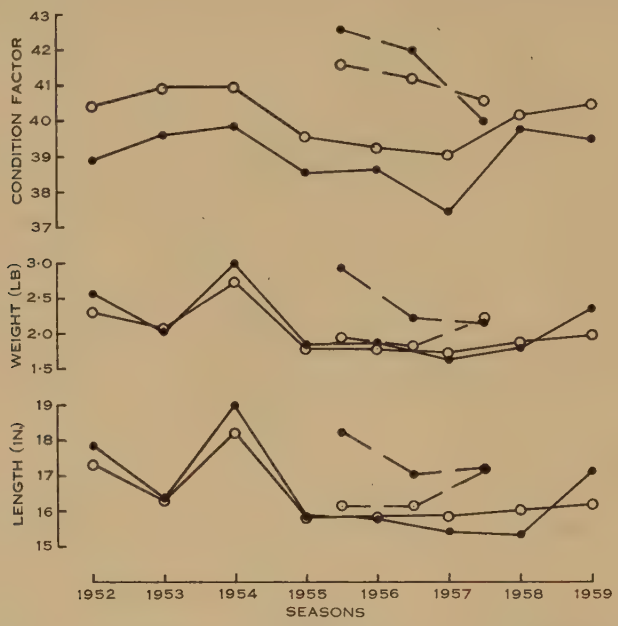


Fig. 4.—Mean length, weight, and condition factor of fish from the spawning runs, taken in the Plenty River trap. The broken lines refer to the summer runs. ●———● males; ○———○ females.

significant because of the changed relation. This differential growth rate is best brought out by a comparison of the cumulative percentage increments based on their respective lengths at $L_1$, shown in Figure 6. The winter run fish are represented by their length at each winter from $L_1$ to $L_6$ in the four year classes of 1949–1952 inclusive in the pooled runs of 1955 and 1956. The summer run fish are represented by the comparable values found in the 1955–56 run. The cumulative percentage increments show that the fish of the summer run have a much higher growth rate up to the end of their fifth year at which time their mean length was 5·3 times that at the end of their first winter whereas in the winter run fish it was only four times the corresponding length. This is discussed below (Section II(*d*)).

(v) *Mortality Rates.*—From the values given in Table 7 mortality rates can be calculated for each age group from four years upwards, using percentage figures in order to make numbers comparable from year to year. These indicate a relatively small mortality between the fourth and fifth years—averaging only 12%; from the

fifth to sixth years the mean value is 60·3%; in the seventh year it is 66·2%, and in the eighth year 64·8%. These figures yield no information on mortality in the early years and indicate an unexpectedly low rate in the fifth year, and a mean rate of about 60% per annum from the fifth year onwards, which in general is confirmed by the results of tagging (Section II(*b*)(v)). Mortality rates calculated from the survivors of individual year classes in successive years are very variable and yield no constant results. The mean for all years in all year classes, however, is a little above 60%.

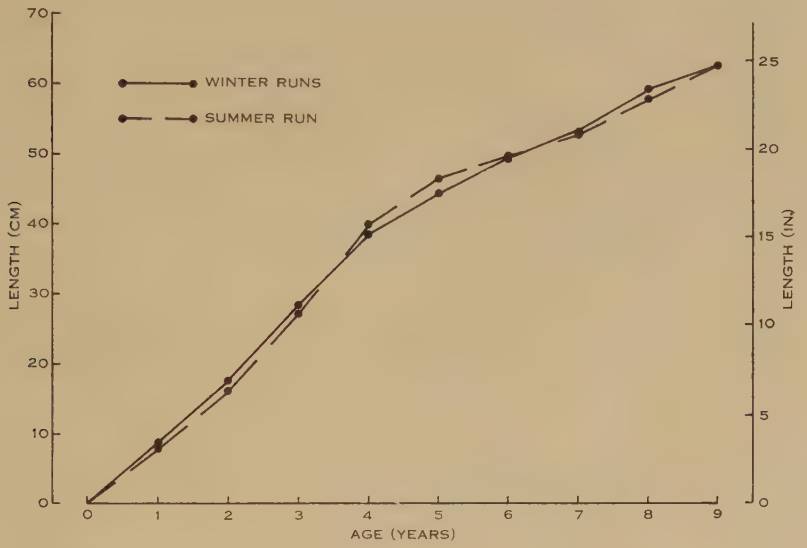


Fig. 5.—Mean lengths-for-age of fish in the Plenty River spawning runs during winter and summer.

Mortality in the population of the Plenty River can also be assessed from the results of sampling by electro-fishing on two occasions early in 1955, when sections of the river above and below the hatchery about ½ mile apart were fished. Since only a fortnight separated these two operations the results have been combined. In a total distance of 245 yd, with an average width of 25 ft, the catch of brown trout was 179: 107 of 0+, 41 of 1+, 18 of 2+, 12 of 3+, and 1 of 4+ fish. The number of 0+ fish should be increased to 160 to correct for the efficiency of the method (Nicholls 1958*c*). The mortalities shown by the corrected figures (74, 56, 33, and 92% respectively) apply to young fish, less than 4 years of age, and show an average not far from 60%, omitting the value for 4+ fish of which only one was taken. The earlier figures relate to the population of upstream migrants at spawning time whereas the present figures relate to the resident population 6 months after spawning. It cannot be claimed that these two samples are truly representative of the whole river since it is likely that larger fish are to be found in greater abundance downstream and smaller ones upstream. The number of upstream migrants at spawning varied from year to year, and the spawning potential was estimated at 300,000 in 1952, 200,000 in 1953, and 400,000 in 1954, after allowance had been made for the

ova stripped during the spawning runs (Section II(*c*)(v)). It can be estimated that in January 1955 the 1954 spawning would have yielded 5500 0+ fish, the 1953 spawning 1100 1+ fish, and the 1952 spawning 640 2+ fish; the 1951 run was not completely checked. These figures are in the ratio of 8·6 to 1·7 to 1 whereas the comparable figures for the electro-fishing samples are 8·9 to 2·2 to 1. These two sets of figures are similar and lead to the conclusion that, allowing for the efficiency of the method, the samples taken by electro-fishing indicate a population with a mortality up to 4 years of age similar to that found for 5-year and older fish in this river system.

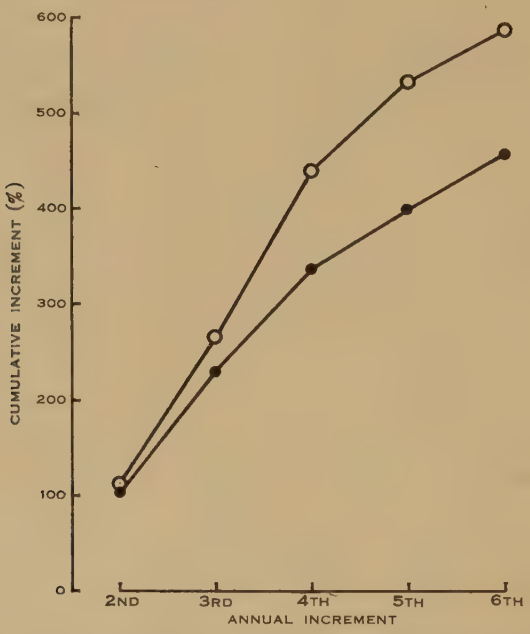


Fig. 6.—Cumulative percentage increments based on the length at the end of the first winter of fish from the summer and winter runs in the Plenty River. ●———● winter runs; ○———○ summer run.

This gives no indication of the mortality during the fifth year, which appeared to be very low (12%) and it must be assumed that 4-year fish were not truly represented in the run of upstream migrants and the rate during the fifth year is similar to that for older and younger fish.

(vi) *Population Estimates and Reproductive Potential.*—Ricker (1958, Ch. 3) shows that there is a relation between the number of tagged fish released into a population, the number recaptured, the total number of fish taken in a sample, and the total population. The estimated population $N$ is calculated from the equation $N = MC/R$ where $M$ is the number of fish marked; $C$ is the number of fish captured; and $R$ is the number of marked fish in the sample. Since 104 tagged fish were released during the spawning run of 1951, eight of these were taken by anglers during the 1951–52 season, and the estimated total catch for that season based on anglers'

returns (Table 5) was 13,000, the estimated total population for the Derwent River System is 169,000. Since all these fish were spawning fish of takable size, this estimate must apply to the population of takable fish.

From the numbers of fish ascending the Plenty River, using the length frequencies of the females passing through the trap, and applying the equation $\log N = 3 \cdot 118 (\log L - 0 \cdot 659)$ calculated for stripped fish in the Plenty River (Nicholls 1958*d*) it is possible to estimate the spawning potential in this river with a fair degree of accuracy. This will yield minimal figures because the egg-counts were the results of stripping mature females, and because of the possibility of fish passing upstream around the trap during periods of flooding.

The results for seven seasons range from 265,000 to 645,000 and give a mean value of about 500,000. Survival has been assumed at 1% for the first year and has been shown to be about 40% per annum thereafter. These figures indicate a total population of about 8500 fish for this river. A varying number of these, estimated at an average of 500 during the three seasons in which they were observed, would be migratory fish and would go to sea as 2+ fish, leaving a resident population of about 8000.

This estimate can be extended to the Derwent River System as a whole on the basis of the relative area of the Plenty River Basin to that of the whole System. The former occupies an area of about 100 sq. miles whereas the total area drained is about 3700 sq. miles, so that the spawning potential in the Derwent System is in the region of 18 million, yielding an estimated population of 300,000 fish of all ages. This estimate applies only to the rivers and does not include the lakes, of which there are several of considerable magnitude, where the population will be much denser. It also omits from consideration the majority of 3-year fish which would almost certainly have spawned, but as residents in the river did not necessarily participate in the upstream migration which is presumably mainly fish from the estuary. Table 7 shows that the proportion of 5-year and older fish, based on the means for five seasons, are in approximately correct proportions for a 40% survival, from which it may be inferred that the 4- and 3-year fish are not truly represented. Correction of the figures for fish of these ages would indicate an annual spawning population of about 1700 fish, of which about 1000 would be females yielding an approximate total of one million ova. Extending this estimate to the Derwent River Basin as a whole would assess its reproductive capacity at about 37 million ova per annum which would yield a total population of about 560,000 fish of all ages, of which approximately 100,000 would be takable. This is lower than the estimate derived from the release of tagged fish, but both sources are subject to errors and the truth may lie somewhere between the two estimates.

(vii) *Conditions Influencing the Spawning Run.*—Rainfall and temperature records have been kept at the Salmon Ponds for many years. A study of these in relation to the spawning runs in the Plenty River shows the following points. Rainfall in the area, represented by 0·20 in. recorded at Salmon Ponds, is sufficient to cause the river to rise and the fish to run. If as much as 2 in. falls during one week there is every probability that the river will rise sufficiently to flood the trap.

Fish will not run until the mean daily temperature falls below 50°F (10·0°C) and will cease running if it falls below 40°F (4·4°C). These figures apply to the normal winter runs, but not to those of the summer. It should be noted that water temperatures taken in the river vary by no more than 2°F from readings in the hatchery boxes where temperatures have always been recorded. Since the water supply to the hatchery flows through an open channel for about ½ mile the temperature in the hatchery will tend to be higher than in the river on warm days and lower on cold days.

In the summer the temperature range during which runs have occurred has been from 50 to 70°F (10·0 to 21·1°C) but there does not appear to be any close relation between the occurrence of a run and temperature or rainfall. The best run (1955–56) occurred during December and January when temperatures varied from 52 to 70°F and the 5·28 in. of rain was evenly divided between the two months though not evenly distributed, and there was no obvious response to rainfall other than that rain had fallen. In 1956–57 (November to January) the mean daily temperature varied from 47 to 65°F (8·3 to 18·3°C) during the run with no apparent response to or dependence upon rainfall. In 1957–58, the poorest year, runs occurred on only eight days from December to March at temperatures between 44 and 60°F (6·7 and 15·6°C) and were always related to rainfalls of at least 0·20 in. though they did not always occur as an immediate result of such falls.

### (*d*) *The Summer Runs*

At this point it is of interest to study the fish of the summer runs since they show characteristics which differ from those of the winter runs. Their age distribution in the only season in which scales were taken, given in Table 7, shows that 3+ fish formed the bulk of the run, the percentage of 4+ and older fish being much smaller than in the winter runs. Even if allowance is made for the fact that they ran towards the end of the growing season and, having almost completed a year's growth, were equivalent to 4-year fish, they were still relatively more numerous than the 4-year fish of any winter run and the older fish much less numerous than those of corresponding ages. In spite of the majority being 3+ fish, the average size of all fish in this run was larger than the average of all fish in the winter runs at that time (Fig. 4). This apparent anomaly is due to the faster rate of growth in fish of the summer run, shown in Figure 6. Since the cross-over takes place in the fourth year of life (Fig. 5) it is not surprising that 3+ fish of the summer run, which have completed most of their year's growth, should be larger than 4-year fish of the winter runs. Since the fish all live under similar conditions it is probable that the differential growth rate is an inherent character and it would appear that they are of different stock from the winter run fish.

There is other evidence in support of this. In October 1951 a large number of young fish was found in the race leading from the Plenty River to the hatchery. These were different in appearance from the normal river fish, having a silvery covering on their scales which hid the underlying marking of the young fish and was easily rubbed off. It was reported that the appearance of these fish in late September or more often in October under similar circumstances was a not unusual occurrence,

varying in extent from year to year. A sample of 104 of these fish was weighed, measured, and scaled, of which 98 were tagged before release in the Plenty River together with an additional 157 marked by finclip only. As shown in Table 2 not one of these fish has been recaptured.

These fish were all 2+ years, with a mean length of 17·0 cm (range 14·1–22·4 cm). Near the end of October and early in November in 1953 another 85 fish were captured in the same way: eight of these were 3+ fish, with a mean length of 19·4 cm (17·5–27·0 cm); 71 were 2+ fish with a mean length of 18·0 cm (14·5–23·0 cm) and 6 were 1+ fish with a mean length of 17·1 cm (15·5–19·5 cm). The 1+ fish were unusually large as yearlings. A downstream trap was installed about this time to catch these fish in larger numbers but being of a temporary nature proved difficult to maintain owing to the uneven flow of the river, and was unsuccessful. In 1954 the trap was again installed and despite maintenance difficulties due to river freshes, 272 fish were taken between October 28 and November 12, of which four were blackfish, *Gadopsis marmoratus* Richardson, and nine were non-migratory trout, trapped during random movements. No scale samples were taken from these fish, which had a mean length of 18·3 cm (14·5–24·0 cm) which by comparison with the 1953 sample indicates that they may all have been 2+ fish. A further sample of 76 was obtained from the race in October 1958, of which 2 were 3+ fish (29·0 and 34·0 cm); and 74 were 2+ fish with a mean length of 18·9 cm (14·0–24·5 cm).

The existence of this downstream migration of fish in the early spring in the Plenty River was first noted in 1874, as recorded in the Salmon Commissioner's Report for 1878 (Tasmania, Salmon Commissioners 1879). These fish were assumed to have been salmon because of the greater number of *Salmo salar* ova which had been imported.

The Report states: "During the last four years, towards the end of September or early in October, Salmon smolts have been captured in a water-race leading to the Ponds from the River Plenty, evidently on their way to the Derwent. The fish were beautifully bright and well formed, . . . The Commissioners consider the presence of these smolts in the Plenty conclusive evidence that the parent fish go up that river to deposit their ova; and as many thousands of ova are annually taken from the Plenty for the purpose of distribution throughout the Colony, and for sale to other Colonies, it is now more probable that, in addition to the Brown Trout, both the Salmon and Salmon Trout have become well established in many and widely separated localities in this Colony, and in the neighbouring continent."

The facts relating to the successful importation of Salmonidae are briefly, that in 1864 some 90,000 salmon ova and 1500 brown trout ova arrived in Tasmania, and yielded about 3000 salmon and 300 trout fry. In 1866 there was a further importation of over 100,000 salmon ova and 15,000 sea-trout ova, yielding about 6000 salmon and 500 sea-trout fry. Of both types of trout, the majority of fish was released within their first year, but a few pairs were retained in separate breeding ponds where they were allowed to spawn naturally. These increased in numbers, and their progeny were distributed to various other waters until 1876 when it was observed that the sea-trout were yielding infertile ova; at this point the parents also were released. Brown trout, however, continued to breed in the ponds.

There have been no subsequent introductions of brown trout, and although there is a gap in the Reports of Commissioners from 1893 to 1908, during which there may have been further importations of salmon and sea trout, the next recorded introduction of sea-trout occurred in 1928 when local anglers endeavoured to establish the sea-trout under the impression that no such fish existed in Tasmania. It is clear from earlier reports, however, that such stocks were well established in the early years and had been mistaken for salmon, which, it would appear, never really became established, in spite of "authoritative" identifications of certain fish as true salmon.

The Report of the Royal Commission on the Fisheries of Tasmania (Tasmania, Royal Commission on Fisheries 1882) provides information absent from earlier reports to the effect that while the brown trout ova came from the Wey, and the Itchen and its tributaries, the sea-trout came from the River Tweed. It also states that *Salmo fario* was abundant and increasing and the establishment of *S. trutta* an accomplished fact. Further, that in 1880 three samples of salmonids were sent to Dr. Gunther at the British Museum, as follows:

(1) from the breeding ponds, thought to be *S. trutta*,

(2) smolts from the downstream migration,

(3) fish caught in the Derwent 35 miles below the breeding ponds.

Dr. Gunther reported that while (1) was undoubtedly a young salmon, (2) and (3) were equally certainly *S. trutta*. It is difficult to understand how a young salmon could have been found in the breeding ponds in 1880 since none was retained there for breeding and there had been no importation of ova since 1866. The alternative (apart from a misidentification) is that salmon had spawned in the Plenty and the young had made its way into the ponds in the same way as the *S. trutta* which undoubtedly formed the bulk of the spring downstream migration.

During the succeeding years two more shipments of salmon ova arrived in Tasmania; 80,000 in 1884, 160,000 in 1885, and "large numbers" in 1888. Yet in spite of the total of nearly half a million salmon ova that were imported it is almost certain that none has survived. The failure to establish this species may be attributed in part to the relatively low survival of ova to reach fry—about 45,000 from the first four shipments and an unknown number from the last; to the majority of these having been released as fry; and to the intervals between successive shipments such that the five successful importations spanned a period of 25 years.

The well-known zoologist, W. Saville Kent, who was Fisheries Inspector in Hobart and Superintendent of the Hatchery from 1884 to 1889, suggested that sea temperatures were too high for salmon. He drew attention to the failure to establish salmon in the rivers of southern France flowing into the Mediterranean stating that the young fish throve while in the rivers, but that after going to sea they disappeared. In the absence of sea temperature records for Tasmanian waters he showed that air temperatures compared closely with those of the south of France.

Mr. F. G. Richmond, of the Solway Fisheries, Dumfries, in a letter to Dr. Terence Butler of Hobart, written in 1952, gave the following reasons for the greater probability of success with sea-trout as against salmon: the very heavy loss incurred

during sea life (in the Atlantic salmon probably 95% loss between smolt and maturity) the factor of "divided migration" by which the fish resulting from one spawning return not all together but over a series of years, at least four years; only a small percentage spawn more than once.

*S. trutta*, however, seems to have become established after the first introduction in 1866, from ova taken from the River Tweed, and the second introduction in 1928, from the Solway Fisheries, may have contributed to the stock. It is of interest to note that Nall (1930, pp. 212–3) with reference to the sea-going habits of the sea-trout, reports that such fish marked in the Tweed were taken as far away as the Dutch banks and Jutland Coast, and that they were reported by the fishermen to have been salmon. The same author distinguishes a number of "local races" of sea-trout. He states (p. 130) that "there is only one species of Atlantic Trout (*S. trutta*) divided by habit into two main forms, migratory and non-migratory". Among the Scottish migratory trout he distinguishes two main groups: one extending up to the east coast (but excluding the Tweed fish as "entirely exceptional" (p. 92)) as far as the Moray Firth, the other along the north-east and north coast and down the west coast. Thus the Tasmanian importations represent the two extremes of the range of Scottish fish. However, he states (p. 133): "these groups correspond roughly with differences in the physical characters of the land and consequently of the rivers". If this is the major influence in the differentiation of local races it is to be expected that in due course, in their new environment, fish introduced into Tasmania would all acquire the same habits irrespective of whether they originated on the east or west coast of Scotland, though maybe differing somewhat from those of their parents.

With reference to the Tweed sea-trout Nall (p. 144) states the principal runs are in summer and autumn, also that 70% of the smolts migrate after 2 years of river life, 20% after 3 years; the average length of the 2-year smolts is 7·2 in. (18·3 cm) and of the 3-year smolts 8·5 in. (21·6 cm). Also (p. 141) that Tweed sea-trout show a tendency to spawn only in alternate years whereas most sea-trout are annual spawners when they have once reached maturity. In the Solway (p. 98) the principal runs are in May and June, though they may be taken at river mouths in March and April (early spring to early summer).

Mr. Richmond, in the letter referred to above, states that sea-trout are distinguished from river trout by their characteristic of migrating to sea as 2-year smolts followed by a return to fresh water after 2–5 months of sea life, at which stage they are known locally as "herlings".

The composition of the samples of downstream migrants taken in the Plenty River in 1953 was 9% of 3+; 84% of 2+, and 7% of 1+; the 2+ fish predominate as they did in the 1951 and 1958 samples. The composition of the upstream summer run in 1955–56, as given in Table 7, shows a predominance of 3+ fish with 2+ and 4+ fish in smaller numbers, the three being represented in similar proportions to those of the 1+, 2+, and 3+ fish of the downstream migrants sampled in 1953; ignoring the older fish the respective percentages are 14, 67, and 19. If the summer runs encountered in the Plenty River are the return of the downstream migrants, then they must have spent over a year in the sea instead of the few months as described by Nall, since it is mostly 2+ fish which go to sea in spring, and 3+ fish

which return a few months later. The mean length at the end of the second winter of the fish of the summer run, as shown in Figure 5 (16·1 cm), is consistent with that of the length at capture of the downstream migrants in spring in the 1953 sample, in which the mean of $L_C$ of the 2+ fish was 18·0 cm and the mean $L_2$ was 15·7 cm.

It has hitherto been generally accepted that sea-trout and river trout are varieties of the same species, showing differences only in habit. If the differences in habit shown by these fish in the Plenty River, which exhibit features characteristic of the sea-trout described by Nall, are any indication of the presence of both varieties, then the history of the introduction of trout into Tasmania at least supports the possibility. River trout were first introduced followed by sea-trout on two occasions, from different sources. If Nall is right in ascribing the differences between the Tweed and Solway sea-trout to differences in the nature of the rivers then it is to be expected that after their introduction to Tasmania and release in the Plenty River fish from both sources would tend to lose their distinguishing characters and acquire habits suited to the changed environment—even possibly to the extent of omitting the "herling" return to fresh water and only reappearing as maiden fish of 3+ years. The gonads of some of these fish were examined and were found to be in the state of development of fish expected to spawn in the coming winter.

In view of the possibility of sea-trout, as distinct from river trout, having become established in the Plenty River, a sample of downstream migrants was compared with a sample of fish known to have been taken from the Great Lake, and of similar age, for a study of meristic characters. The Great Lake fish were reared in the hatchery, which receives its water from the Plenty River in which also the downstream migrants were hatched; the latter were almost certainly reared at a higher altitude than that of the hatchery and may reasonably be assumed therefore to have hatched at a lower temperature than did the fish in the hatchery. Vertebral counts were made on 118 fish reared in the hatchery and on 76 downstream migrants; ray counts were made in the dorsal, anal, ventral, and pectoral fins. The results are given in Table 8.

Schmidt (1921) showed that the number of vertebrae in sea-trout varies with the temperature of development. Taaning (1944), also working with sea-trout, confirmed and extended this work, rearing young from the same parents under constant temperature conditions, at 3, 6, and 9°C. He found that the highest number of vertebrae was produced at both the low and the high temperatures, the lowest number being found when development proceeded at about 6°C. The number of rays in the dorsal and pectoral fins increased with rising temperature within the range studied, whilst the average number of anal fin-rays showed only slight differences with temperature.

There is a significant difference between the vertebral counts found in fish from the two sources in the above table. There is every reason to believe that the downstream migrants were hatched at a higher altitude than the hatchery-reared fish and would thus have been exposed to lower water temperatures. Since they show a higher vertebral count it follows from Taaning's work only that they could have developed at either a higher or lower temperature than the hatchery-reared fish. Mean water temperatures at the hatchery during the probable period of development

were 4·5°C, and since this was likely to have been higher than temperatures upstream in the Plenty River, this factor could have accounted for the difference in vertebral count; but Taaning's work also showed that for dorsal and pectoral fin-ray counts there was a steady increase with rising temperatures from 3 to 9°C, from which it follows that the downstream migrants, hatched at the lower temperatures, should have lower counts than the hatchery-reared fish. The results show the reverse; in every case of fin-ray counts (except the ventral fins) the downstream migrants have the higher count which is statistically significant except for the pectoral fins. Taaning did not report on the ventral fins.

TABLE 8

MERISTIC CHARACTERS OF DOWNSTREAM MIGRANTS AND HATCHERY-REARED FISH

| Source | No. of Counts | Mean Counts | Standard Deviation | *t* |
|---|---|---|---|---|
| | | *Vertebral Counts* | | |
| Hatchery-reared | 118 | 57·03 | 0·591 | 2·673 |
| Downstream migrants | 76 | 57·30 | 0·746 | |
| | | *Dorsal Fin-Ray Counts* | | |
| Hatchery-reared | 105 | 14·53 | 0·717 | 3·253 |
| Downstream migrants | 73 | 14·89 | 0·567 | |
| | | *Anal Fin-Ray Counts* | | |
| Hatchery-reared | 102 | 12·39 | 0·744 | 3·911 |
| Downstream migrants | 73 | 12·82 | 0·509 | |
| | | *Ventral Fin-Ray Counts* | | |
| Hatchery-reared | 210 | 9·31 | 0·412 | 5·167 |
| Downstream migrants | 146 | 9·08 | 0·265 | |
| | | *Pectoral Fin-Ray Counts* | | |
| Hatchery-reared | 207 | 13·94 | 0·430 | 1·796 |
| Downstream migrants | 145 | 14·05 | 0·505 | |

These results are not consistent with a difference in temperature as the cause of the meristic variation and it follows that unless the differences were due to other causes arising from faults in technique or causes not apparent, they are possibly of genetic origin related to distinct races of *S. trutta*. This conclusion receives strong support from the difference in the number of anal fin-rays since Taaning found no real difference in these fins due to temperature.

It seems probable, therefore, that the migratory and non-migratory brown trout found here are at least racially distinct and have survived as two distinct populations since their first introductions. However, the problem requires further study under conditions of carefully controlled experiments, using the downstream migrants as one source and, as the other source, river fish taken from the natural habitat

situated above waterfalls which are natural barriers to upstream migration. This could be expected to supply a pure population of non-migratory fish provided it had not been recently stocked with hatchery-reared fish which might well be a mixed stock or even contain hybrids as a result of stripping operations in the hatchery. It also seems probable that the summer runs of upstream migrants are composed of sea-trout returning to fresh water for spawning.

TABLE 9

RESULTS OF ELECTRO-FISHING IN PLENTY RIVER

| Results | Site | | |
|---|---|---|---|
| | I | II | Combined |
| Length of section (ft) | 433 | 302 | 735 |
| Mean width (ft) | 24·8 | 25·4 | 25·1 |
| Mean depth (in.) | 13·9 | 11·4 | 12·9 |
| Number of fish taken | | | |
| Brown trout | 111 | 68 | 179 |
| Rainbow trout | 3 | — | 3 |
| Eels | 63 | 23 | 86 |
| Other species | 24 | 9 | 33 |
| Weight of fish taken (lb) | | | |
| Brown trout | 12·60 | 3·52 | 16·12 |
| Rainbow trout | 0·06 | — | 0·06 |
| Eels | 4·94 | 3·13 | 8·07 |
| Other species | 1·94 | 0·25 | 2·19 |
| Weight of fish (lb) per acre | | | |
| Brown trout | 51 | 20 | 38 |
| Rainbow trout | — | — | — |
| Eels | 20 | 18 | 19 |
| Other species | 8 | 1·5 | 5 |
| Total | 79 | 39·5 | 62 |

### (*e*) *Electro-Fishing within the System*

At three different places in the rivers of the Derwent River System electro-fishing has been carried out. These were in the Plenty River in January and February 1955; in the Derwent River above Lake King William in February 1955, and in the Clyde River at Bothwell in December 1955.

(i) *Plenty River.*—Reference has already been made to operations in the Plenty River and it remains only to summarize the data omitted. At the first site, on January 25, the section of river fished consisted of about 130 ft of steady river of mean width 26·5 ft and mean depth 5·25 in., followed by a pool about 180 ft long, 25 ft in mean width, and 20 in. in mean depth; then a short section about 40 ft, 22 ft wide and 10·5 in. deep, and the final section a pool of about 100 ft having a mean width of 22 ft and mean depth of 16·2 in. The bottom was of gravel suitable for spawning;

logs were present, and the banks were undercut and carrying overhanging scrub, thus providing refuge for the fish and protection from angling. The river level was very low, below normal for the time of year, only 0·29 in. of rain having been recorded during the previous 40 days. The second site, further upstream, fished on February 10, consisted of a long pool of steady water shallowing over a short stretch of about 50 ft. The bottom was of good spawning gravel; there was good cover and protection for fish similar to that of the lower section. The river level was still below normal, only 0·63 in. of rain having been recorded since January 25, of which 0·57 fell during the last six days of January. Water temperatures on both occasions were fairly high, about 70°F on January 25 and 64°F on February 10. The remaining data are presented in Table 9. At Site I the three rainbow trout were 0+ fish; the eels varied

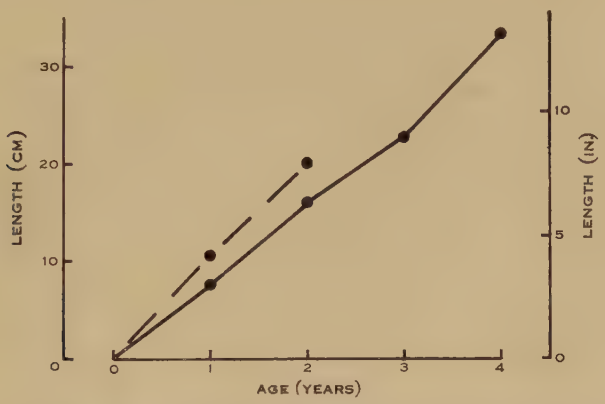


Fig. 7.—Mean lengths-for-age of fish taken from the Plenty River by electro-fishing in 1955. ●———● Site I; ●— — —● Site II.

from 4 to 20 in. in length, and the other species were 22 freshwater flatheads (sandfish or pike) (*Pseudaphritis d'urvillei* C. & V.) and two small *Galaxias* sp. At Site II the eels were of a similar size range and the other species were four blackfish, *Gadopsis marmoratus* Richardson, one freshwater flathead, one large *Galaxias* sp., and three small lampreys (unidentified). The scale samples taken from these fish yield the data given in Figure 7, in which results for each site have been given separately because of differences in growth rate. It is evident that at Site I growth follows very closely on that shown in Figure 2 for the Plenty River, based on samples taken by anglers. At Site II a better growth rate is shown which may be directly related to the less dense population. The condition factor closely resembles that for the fish taken by anglers from this river.

It is clear that there is some variation in the carrying capacity of this river, and on only two samples it is unwise to generalize with regard to the river as a whole, but the sections sampled show moderately good weights of trout per acre when compared with other Tasmanian trout streams (Nicholls 1958*a*, 1958*c*). The quantity of eels is fairly high and it would seem that the trout population would benefit by the removal of these competitors.

(ii) *Derwent River.*—As this section of river lies between Lakes St. Clair and King William, and from the fishery aspect is regarded as part of the lakes, consideration of the results of electro-fishing operations here will be deferred to the appropriate paper.

(iii) *Clyde River.*—This river, and some of its tributaries, were fished at five places in the vicinity of Bothwell on December 14 and 15, 1955. These operations were carried out at the request of the local branch of the Anglers' Association. The results are given in Table 10, in which the sites are as follows: I, Norwood Creek; II, a mill race on the Clyde River; III, the Clyde at Cluny Creek; IV, the Clyde in

TABLE 10

RESULTS OF ELECTRO-FISHING IN CLYDE RIVER

| Results | Site | | | | |
|---|---|---|---|---|---|
| | I | II | III | IV | V |
| Length of section (ft) | 263 | 444 | 234 | 365 | 262 |
| Mean width (ft) | 10·6 | 13·2 | 21·6 | 25·6 | 25·0 |
| Mean depth (in.) | 9·5 | 8·8 | 21·6 | 15·6 | 16·1 |
| Number of fish taken | | | | | |
| Trout | 4 | 9 | 19 | 43 | 3 |
| Eels | — | 2 | 3 | 8 | 6 |
| Tench | — | — | — | 14 | — |
| Weight of fish taken (lb) | | | | | |
| Trout | 0·50 | 1·77 | 1·59 | 7·89 | 0·41 |
| Eels | — | 4·56 | ? | 6·03 | 1·78 |
| Tench | — | — | — | 2·02 | — |
| Weight of fish (lb) per acre | | | | | |
| Trout | 8 | 13 | 14 | 37 | 3 |
| Eels | — | 34 | ? | 28 | 12 |
| Tench | — | — | — | 9 | — |
| Total | 8 | 47 | 14 | 74 | 15 |

he township of Bothwell, between the two swimming pools; and V, the Clyde at the racecourse. The figures show that the best section of river was that in the township, carrying 36 lb of trout, 10 lb of tench, and 28 lb of eels to the acre; the total of 74 lb per acre indicates a good carrying capacity at this point. Of the trout population 2% were 3+ (31·3 cm); 12% were 2+ (24·3 cm); 84% were 1+ (17·5 cm), and 2% were 0+ fish (5·1 cm). The 3+ fish, and four of the 2+ were of takable size, and the fifth would have been takable by the end of the season (14% of population takable). The ratio of 3+ to 2+ fish indicates an 80% mortality including that due to angling, and the ratio of 2+ to 1+ indicates a higher mortality, but the 1+ population had not been subjected to angling. If the 80% mortality applied also to this age group then that portion due to angling can be assessed at 30%. The low number of 0+ fish indicates that this section of stream was not suited to the survival of young fish.

Sites I and II were fished in the expectation of finding nursery areas, but the first (Norwood Creek) was too exposed and unsuitable as a nursery area, yielding only three 0+ fish. Site II (the Mill Race) appeared more suitable but carried no 0+ fish. Site III (the Clyde at Cluny's Creek) carried a population of three 2+ and 15 1+ fish, showing a 20% survival from 1+ to 2+. All fish in this section were smaller at $L_1$ than in any other section, and their condition was also the lowest found. The small population found at Site V could be accounted for by its open nature and its having been subjected to heavy fishing.

Of the total weight of fish taken in these sections about 47% was eels. It can hardly be doubted that the removal of these competitors with trout for food would benefit the trout population in growth and condition, and might influence survival.

## III. The Huon River System

### (*a*) *Environmental Characteristics*

The Huon River is over 70 miles in length, measured to Ranclagh (about 2 miles above Huonville, the major township of the district) at which point it is assumed to discharge into its estuary. It has several large tributaries, mostly draining the upper regions of its basin which is located in the uninhabited south-western portion of Tasmania. As it approaches the coast, and throughout its estuary, it receives numerous smaller tributaries, all of which lie in the settled area and are subject to fishing. The approximate area of the Huon basin is 1200 sq. miles of which not more than one-third is readily accessible to anglers, so that most of the fishing is concentrated in the lower reaches of the river and the tributaries of that area. Portion of this lower region is relatively densely settled, the land being devoted to orchards. It is a region of fairly high rainfall, 30–40 in. per annum in the inhabited area, rising probably to 80–90 in. per annum in the upper reaches. River flow measurements at Frying Pan Creek, about 15 river miles upstream from Huonville, show that the mean monthly flow from 1922 to 1959 was 3255 cu. ft/sec (range, 210 to 76,000).

### (*b*) *Results and Discussion*

(i) *The Daily Catch.*—Returns varying from two to eleven per season are available over ten seasons. No attempt has been made to analyse these returns for tidal and fresh water fishing because of the low numbers which scarcely warrant statistical analysis. However, Table 11 gives the usual data for the combined fishery and shows that there was a seasonal fluctuation from 1·3 to 3·4 fish per angler per day during the decade. No specific trend is observable in these figures and statistical analysis shows that there is no significant difference between the seasons during the period. The rate of catch appears to be rather similar to that from the Derwent River System.

(ii) *Fish Lengths.*—Although the total number of fish measured by anglers from this System since 1949–50 was low, an analysis would have little meaning if tidal and fresh water fish were not distinguished, because of the different minimal lengths operating for each. From tidal waters 100 fish lengths are available from five seasons and from fresh waters, 288 lengths during six seasons. The mean values are

plotted in Figure 8. The differences in tidal waters are not statistically significant but those for fresh water are. The latter show a downward trend over the later years but the numbers of fish involved are too few to yield reliable conclusions.

TABLE 11

MEAN DAILY CATCH PER ANGLER FROM THE HUON RIVER SYSTEM

| Season | Number of Fish | Number of Days | Fish per Day |
|---|---|---|---|
| 1945–46 | 142 | 42 | 3·38 |
| 1946–47 | 19 | 7 | 2·71 |
| 1947–48 | 29 | 17 | 1·71 |
| 1948–49 | 20 | 9 | 2·22 |
| 1949–50 | 78 | 41 | 1·90 |
| 1950–51 | 201 | 85 | 2·36 |
| 1951–52 | 14 | 11 | 1·27 |
| 1952–53 | 57 | 31 | 1·84 |
| 1953–54 | 44 | 14 | 3·14 |
| 1954–55 | 23 | 9 | 2·56 |
| 1945–46 to 1954–55 | 627 | 266 | 2·36 |

(iii) *Growth and Age.*—From this district, during two seasons, 146 scale samples were available for study; 17 in 1949–50, and 129 in 1950–51. The samples came

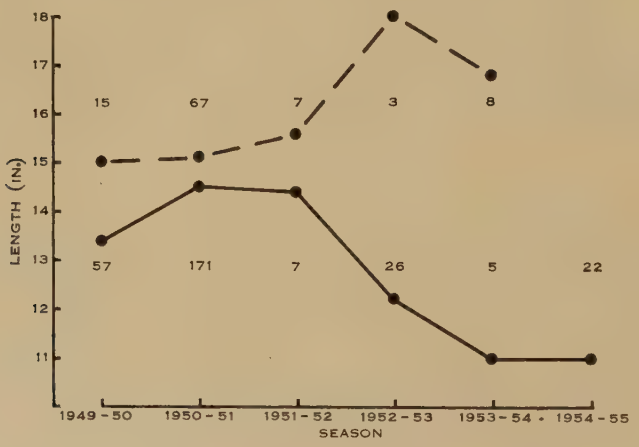


Fig. 8.—Mean lengths of fish from the Huon River System from 1949–50 to 1954–55. ●— — —● from tidal waters; ●———● from fresh waters. The numbers of fish measured in each season are given on the graphs.

almost wholly from tidal waters of the Huon and Esperance rivers, and since there was no statistically significant difference in the growth rates between these sources

the data have been pooled. There were differences which were significant as between seasons but because there were so few fish for the earlier season all were pooled to yield mean values for this district. These are shown in Figure 9. The graph shows a steady growth rate up to 6 years of age similar to that of fish from tidal waters of the Derwent River System (Fig. 2).

(iv) *Condition.*—The mean values for all fish from each age group from the pooled sources and seasons are shown in Figure 9. The usual feature of decrease in value with increasing age is evident. Fish from this district appear to have somewhat higher values than those from the Derwent River System (Fig. 2).

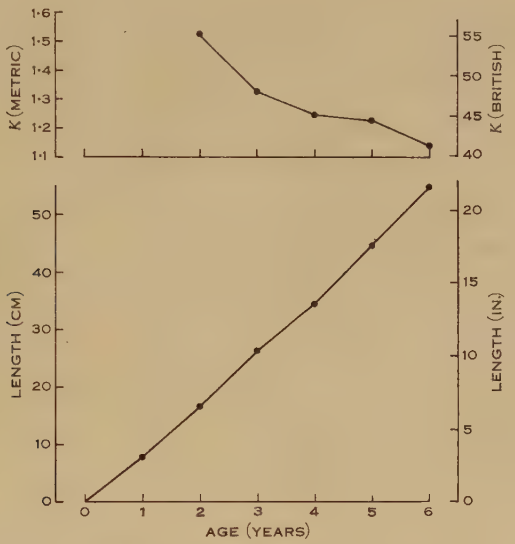


Fig. 9.—Mean lengths-for-age and condition ($K$) of fish from tidal waters of the Huon River System.

(v) *Mortality Rates.*—Insufficient information is available to enable valid estimates of mortality rates to be calculated for this district.

(vi) *Annual Catch per Angler.*—The results of the analysis based on all returns recording fishing in this System are given in Table 12. The differences between the seasonal means are not statistically significant. The very high values for 1947–48 and 1948–49 are traceable to one angler who reported his catches in those two seasons only. When these catches are omitted, catches for these seasons fall into line with the general run (values given in brackets); and the slight downward trend shown by the regression line is clearly not significant. It is clear that the values given are minimal since this angler (and possibly others) probably fished every season with similar success, so that the figures for this district are not truly representative.

(vii) *Estimated Total Catches.*—These have been calculated from the data available, excluding the two catches taken by one angler in successive seasons, referred to in the preceding paragraph. The results are given in Table 13 but must be regarded as minimal and accepted only with caution as the data are not truly representative.

The estimated total catches over the period suggest an average annual catch of nearly 4000 fish from the System and no increase in later years correlated with the steady increase in the number of licensed anglers.

(viii) *Summary.*—The data from this district are very meagre, but there is no indication of any change in the daily catch rate per angler over the period studied. It is probable also that there has been no change in the mean length of fish caught by anglers, a fact which suggests that the fishery is stable. Although the average

TABLE 12

MEAN ANNUAL CATCH PER ANGLER FROM THE HUON RIVER SYSTEM

In the values given in parentheses, the returns from one exceptionally successful angler are omitted

| Season | Number of Anglers | Number of Fish | Fish per Angler |
|---|---|---|---|
| 1945–46 | 6 | 152 | 25·3 |
| 1946–47 | 2 | 18 | 9·0 |
| 1947–48 | 5 (4) | 372 (46) | 74·4 (11·5) |
| 1948–49 | 3 (2) | 219 (17) | 73·0 (8·5) |
| 1949–50 | 9 | 73 | 8·1 |
| 1950–51 | 13 | 247 | 19·0 |
| 1951–52 | 5 | 14 | 2·8 |
| 1952–53 | 5 | 48 | 9·6 |
| 1953–54 | 4 | 44 | 11·0 |
| 1954–55 | 3 | 22 | 7·3 |
| 1945–46 to 1954–55 | 55 (53) | 1209 (681) | 22·0 (12·9) |

size of fish taken by anglers from tidal waters of the Huon appears to be somewhat smaller than that of fish from the Derwent, the growth rate in fish from both sources is very similar. The condition of fish in the Huon is good, and somewhat better than that of Derwent tidal water fish. Total catch per angler and estimated total annual catches for the System are of doubtful reliability. No tagged or marked fish have been released in this System during the course of this investigation and the data available are too few to enable mortality rates to be calculated.

The Huon is renowned for occasional specimens of very large fish, and the record fish taken in Tasmanian waters came from this source. It was caught by Sir Robert Hamilton in 1887; it was 35 in. long with a girth of 26 in. and weighed 29 lb. Since then several large fish have been taken at intervals of a few years. In 1950 a female brown trout 32 in. in length, weighing 23 lb, and with a condition factor of 70·2, was taken at Ranelagh. Its scales showed it to have been in its ninth year of life, the lengths at the end of each winter being: 5·9, 7·9, 10·2, 14·0, 16·9, 18·7, 25·0, and 30·9 in.; growth was normal up to the end of its sixth winter and

excessive during the next two years and this good rate was being maintained at the time of capture. When the fish was taken the gut contained 11 lampreys of various sizes. A photograph of this fish has been published by T. C. Roughley (1951, Plate 73).

## IV. Minor Rivers of the Region

There are numerous rivers on the east and south-east coasts of Tasmania, most of which carry trout and are fished by local residents, occasionally visited by anglers from other districts. Three of these may be worth some consideration but records from all are so few as to make detailed statistical analysis of little value.

Table 13

ESTIMATED TOTAL CATCHES FROM THE HUON RIVER SYSTEM

| Season | Estimated No. Fishing in System | Mean Catch per Angler | Estimated Total Catch | Coefficient of Variation | Standard Error |
|---|---|---|---|---|---|
| 1945–46 | 291 | 25·3 | 7360 | 0·698 | 5140 |
| 1946–47 | 107 | 9·0 | 960 | 1·253 | 1200 |
| 1947–48 | 160 | 11·5 | 1840 | 0·602 | 1110 |
| 1948–49 | 237 | 8·5 | 2010 | 1·322 | 2660 |
| 1949–50 | 258 | 8·1 | 2090 | 0·575 | 1200 |
| 1950–51 | 392 | 19·0 | 7450 | 0·132 | 980 |
| 1951–52 | 272 | 2·8 | 760 | 0·718 | 550 |
| 1952–53 | 292 | 9·6 | 2800 | 0·879 | 2460 |
| 1953–54 | 460 | 11·0 | 5060 | 1·060 | 5360 |
| 1954–55 | 469 | 7·3 | 3420 | 0·778 | 2660 |

The Coal River, about 30 miles long, flowing almost due south to enter the sea about 10 miles east of Hobart, provides good fishing. It was visited by 19 anglers on 105 occasions during seven seasons for an average return of 1·8 fish per day's fishing, or nearly 10 fish per angler per season. The size of fish taken ranged from 9 to 20 in. with a mean of 14·2 in.

The Prosser River which lies further to the east, and flows in an easterly direction to join the sea at Orford, about 50 miles from Hobart by road, is somewhat shorter than the Coal and is fished mostly in its estuary whereas the Coal provides good fishing throughout its length as well as in its one main tributary. The Prosser was visited by six anglers on 21 occasions during five seasons and yielded an average return of 2·7 fish per angler per day and nearly 10 fish per angler per season. The higher figure was due mainly to one angler who fished it on four days in October and November in one season, his daily catches being 12, 12, 2, and 11, for 4, 4, 1, and 6 hours' effort respectively. No similar result was achieved on any other occasion although the same angler visited it again in the following season. The lengths of fish taken ranged from 9 to 20 in., with a mean of 13·9 in.

The third river, the North West Bay River, lies about 12 miles to the south-west of Hobart and, draining the western slopes of Mt. Wellington, enters the sea at

Margate, at the head of the bay from which it derives its name. This was visited by seven anglers on 29 occasions during six seasons and yielded a return of 2·8 fish per day's fishing and 11·5 fish per angler per season. The mean length of all fish taken was 12·6 in. (10–18 in.). There was no significant difference in the lengths of fish taken from these three sources.

The rivers are much more extensively fished than the few returns would indicate, but these probably give some indication of the rate of catching and of the size of fish taken.

## V. The Relation between Total Catch and Survivors from Stocking

It is most unfortunate that the estimated total catches cannot be calculated with the same degree of reliability as can the survivors from stocking. Records kept by the Superintendent of the Hatcheries show in detail the number, stage, and place of liberation of all trout for many years. As in previous papers these figures have been used to calculate probable total populations of hatchery-reared fish within the Southern Region, using the usual 1% survival from fry to yearlings, 50% survival for fingerlings, and thereafter applying the average mortality rates disclosed for the particular system: 40% survival per annum in the Derwent River System. The data provided from the anglers' records of this System do not permit an accurate assessment of the proportions of 1- and 2-year fish takable by anglers, so that values found in other parts of the State have been applied, namely 30% of 2-year and 1% of 1-year fish. The results have been summarized in Table 14 and show the mean annual population of takable fish resulting from stocking to have been about 5300 during the 12-year period from 1945–46 to 1956–57. The corresponding mean estimated annual catch is 19,500, showing a ratio of 1 : 20·9. Excluding the figures for 1956–57, which differ markedly from the rest, the ratio is 1 : 2·2 which, if it could be accepted with confidence, would indicate a considerable possible contribution to the fishery resulting from stocking. This is much higher than the mean value found in other parts of the State and is probably due partly to the total catches having been underestimated. Too many factors are in doubt for these figures to be readily accepted; an especial difficulty is the very small proportion of anglers who made returns in this Region: a mean over the 12 years of 29 in a mean number of 1928 licences for the Region, or 1·5%. There is also the evidence from the analysis of the Huon River fishery, as well as from information received personally, that anglers who have taken good catches have not made returns, so that the estimated total catches are too low.

Some interesting facts may be noted from a study of the stocking rates in individual rivers. In the Plenty River, during the 7-year period 1952–1958, when a careful check was made of the spawning fish passing through the trap, it is estimated that 2,753,000 eggs were shed above the trap. This allows for those stripped from some of the fish at the hatchery and yields a mean of 393,285 per annum. Allowing for a loss of 10% between egg and alevin—Allen (1951, p. 95) found a higher rate for the Horokiwi but quotes Hobb's earlier work for other streams—it would be expected that the mean natural production of fry would be about 354,000, of which 3540 would survive to become yearlings.

Figures are available for stocking the Plenty River which show that during the 10-year period 1942 to 1951 the mean number of fish released per annum was 103,700 fry, 2020 fingerlings, and 3432 yearlings. These would represent respectively 1037, 1010, and 3432 yearling fish, a total of 5479 yearlings per annum. Thus the mean annual stocking rate exceeded the mean annual natural production by about 60%. The two periods for which these data are available do not coincide but it may be accepted that natural spawning figures are representative of a long period prior to the actual recording of data, but stripping of fish from this river was not carried out extensively until the installation of the fish trap.

TABLE 14

TAKABLE SURVIVORS FROM STOCKING IN RELATION TO TOTAL CATCH FROM THE DERWENT RIVER SYSTEM

| Season | Takable Survivors | Total Catch | Ratio |
|---|---|---|---|
| 1945–46 | 9675 | 16000 | 1·7 |
| 1946–47 | 5421 | 21000 | 3·9 |
| 1947–48 | 4853 | 12100 | 2·5 |
| 1948–49 | 8900 | 5600 | 0·6 |
| 1949–50 | 10284 | 11000 | 1·1 |
| 1950–51 | 6052 | 15000 | 2·5 |
| 1951–52 | 4024 | 13000 | 3·2 |
| 1952–53 | 3782 | 8600 | 2·3 |
| 1953–54 | 4478 | 8500 | 1·9 |
| 1954–55 | 3489 | 10500 | 3·0 |
| 1955–56 | 1440 | 13500 | 9·4 |
| 1956–57 | 1229 | 97000 | 78·9 |
| Means | 5302 | 19317 | 9·25 |

Ratio of means: 20·9

Of the fish taken in the electro-fishing samples referred to above (Section II(*c*)(v)) 45% of the 2+ and older fish were takable, a figure only slightly lower than that estimated for the North Esk (Nicholls 1958*b*). It would be unwise to estimate even approximately the carrying capacity of a river such as this from the data available since upstream and downstream sections were not studied. It can be assumed that whatever the carrying capacity, the addition of released fish into the existing population would result in a great mortality among the released fish until an approach to a balance was achieved, but it is clear that consistent stocking at a rate as high as that practised during this period could have strained the carrying capacity to its limit and given rise to a population of stunted fish of which an unduly large proportion were below takable size, a condition which according to some anglers who frequented this stream had existed for several years. Even if the survival of released fish in this river was as low as that found for the North Esk, it can

be seen that while the natural population of 3540 yearlings, with an annual survival rate of 40%, would yield 560 3-year fish the 5500 released fish, with a survival rate of only 2% to 3 years, would yield 110 fish of that age, or roughly an addition of one-fifth to the natural population.

From 1952 to 1954 inclusive no fish were released in this stream and by January 1955, when the population was examined, the survivors from the latest release in 1951 should have numbered fewer than 40 4+ fish and 100 3+ fish, with no younger fish. The stream should thus have had an opportunity to recover from excessive stocking and this is shown by the composition of the population at that time. All the 3+ and older fish were takable; 2+ fish present were of a size such that about 70% would have become takable before the end of the season. Fish of takable size were present in the lower section at the rate of 160 per mile, a figure not far short of that found for Sassafras Creek (Nicholls 1958*a*) and considerably better than that for the North Esk (Nicholls 1958*c*). In the upper section no fish of takable size were found but by the end of the season they should have been present at the rate of about 35 per mile.

There can be little doubt that stocking now makes only a minute contribution to the total population and an insignificant one to anglers' catches.

## VI. Acknowledgments

It is impossible to make individual acknowledgment of the assistance received from the many anglers who made returns of their seasons' fishing, but to all of them the author's thanks are due, especially to the members of the Bothwell Branch of the Southern Tasmanian Licensed Anglers' Association, and to all those who contributed by collecting scale samples.

Mr. H. V. Jones, Superintendent of the Hatcheries, and his staff have made valuable contributions in the collection of data in the field, and the Tasmanian Hydro-Electric Commission has supplied data on river flow. This assistance is gratefully acknowledged.

The author is especially indebted to Dr. Terence Butler of Hobart for making available correspondence with Mr. Richmond of the Solway Fisheries concerning the introduction of sea-trout ova in 1928.

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# A REVISION OF THE INLAND WATER GENUS *CALAMOECIA* (COPEPODA: CALANOIDA)

By I. A. E. Bayly*

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*Summary*

The status of the genus is discussed, the synonymy of *Brunella* with *Calamoecia* being upheld, and the synonymy of *Calamoecia* with *Limnocalanus* being rejected. A new description is proposed for the genus which is considered as now containing nine species, one of which is new. A key to species is given for both male and female specimens. Eight of the species are figured and where necessary redescribed. The distribution of the genus and some of the species is discussed, together with some general aspects of their ecology.

## I. Introduction

The genus *Calamoecia* is confined in distribution to Australia and the North Island of New Zealand. Although within this region its species frequently occur as dominants in the plankton of lentic environments, the taxonomy of the genus has not previously been dealt with comprehensively. The greater portion of the present paper is intended to facilitate identification of species of *Calamoecia*, and to thus assist in greater attention being focused on their ecological relationships.

The distribution of localities from which material was obtained for this revision is discussed in Section IV. All New Zealand material and all Queensland material, except that from the Atherton Tableland, was collected by the author. For the availability of all the remaining material, the author is indebted to various people indicated in the Acknowledgments.

## II. Status of the Genus

The genera *Calamoecia* Brady, 1906, and *Brunella* Smith, 1909, were reviewed by Jolly (1955) who declared them synonymous, *Calamoecia* taking precedence. However, this review omitted reference to the fact that Kiser (1947) had previously synonymized *Calamoecia* with *Limnocalanus* Sars, 1863. Brehm (1959) tentatively adopted the synonymy proposed by both Kiser and Jolly, and discussed the zoogeographical problems that would arise should *Brunella* and *Calamoecia* both prove to be synonymous with *Limnocalanus*.

Kiser (1947) correctly pointed out, as did Jolly (1955), that non-geniculate antennules of mature *Calamoecia* are 25-segmented, not 24-segmented as described by Brady (1906). This now constitutes a point of difference from *Limnocalanus*, the antennule of which is considered to be 24-segmented (Wilson 1959, p. 752). However, Kiser's main reason for synonymizing *Calamoecia* with *Limnocalanus* was his claim that in *Calamoecia lucasi* Brady, the endopodites of the first four pairs of

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natatory legs were all 3-segmented, as were those of the female fifth pair. The present author has examined these appendages of not less than 10 male and 10 female specimens of *C. lucasi* from each of eight localities in New Zealand. No specimen was found in which the endopodites of the first pair of swimming feet were more than 1-segmented (Fig. 6*E*) or in which the endopodites of feet 2 to 4 were anything but 2-segmented (Fig. 6*F*). The endopodites of the fifth pair of legs in the female were never more than 2-segmented. This condition is also true of all Australian species of *Calamoecia* that have been examined. Apart from these differences in endopodite segmentation, there are marked differences between *Calamoecia* and *Limnocalanus* in other respects. Thus the ventral bulge in the genital segment of the urosome of the female is more pronounced in *Calamoecia* than in *Limnocalanus*. Furthermore in *Calamoecia*, but not in *Limnocalanus*, the exopodite of the right fifth leg of the male terminates in a long hook extending far beyond the terminal segment of the endopodite. Even allowing for intraspecific and interspecific variation in total body length, there is a marked size discrepancy between the species of the two genera. *Calamoecia* contains small calanoids, the males being usually less than 1·0 mm in length, while in *Limnocalanus* the males are usually not less than 2·0 mm in length (Marsh 1933; Wilson 1959, p. 755). Finally, in *Calamoecia* the eggs are carried in egg sacs (with the possible exception of *C. salina* (Nicholls); see Nicholls (1944)) but in *Limnocalanus* the eggs are apparently laid free in the water (Wilson 1959, p. 747). Although Brady (1906) considered *Calamoecia* to be more closely related to *Limnocalanus* than to any other described genus, both Sars (1908) and Fairbridge (1945*b*) consider *Calamoecia* more closely related to *Boeckella*. Fairbridge (1945*b*, p. 75) points out the strong developmental evidence for a close relationship between *Boeckella* and *Calamoecia*.

It is concluded that *Calamoecia* is a valid genus quite distinct from *Limnocalanus*, and that therefore the zoogeographical situation which Brehm (1959) saw as a possibility does not actually exist. The explanation advanced for the 3-segmented condition of the endopodite shown by Kiser (1947, figs. 1 and 2) is that his drawings are not of *Calamoecia* appendages, but of those of *Boeckella*—probably *B. propinqua* Sars—with which they agree precisely. His figure of the female fifth feet (Kiser 1947, fig. 2) shows the distal segment of the exopodite with seven spines. This is a condition universal in the New Zealand boeckellids (Jolly 1957) but does not normally occur in *Calamoecia lucasi* or any other described species of *Calamoecia*. Presumably his material included a mixed collection of the two genera, for there is no doubt that the male fifth feet illustrated (Kiser 1947, fig. 10) are those of *C. lucasi*.

There is an error in the revised generic description of *Calamoecia* proposed by Jolly (1955) in that, if *Brunella* and *Calamoecia* are to be synonymous, it is not a necessary condition that the endopodite of the fifth right leg of the male should be 3-segmented. This endopodite is 1-segmented in *C. australica* Sars, 1908, and 2-segmented in *C. ampulla* (Searle), 1911, and *C. australis* (Searle), 1911. Neither is it necessary for the endopodite of the female fifth legs to be 2- or 3-segmented, it is frequently 1-segmented and apparently rarely 3-segmented. The latter condition has been reported, as an unusual one, by Jolly (1955) for *C. lucasi*, and by Fairbridge (1945*b*) for *C. attenuata*, but has not been observed by the author. The revised

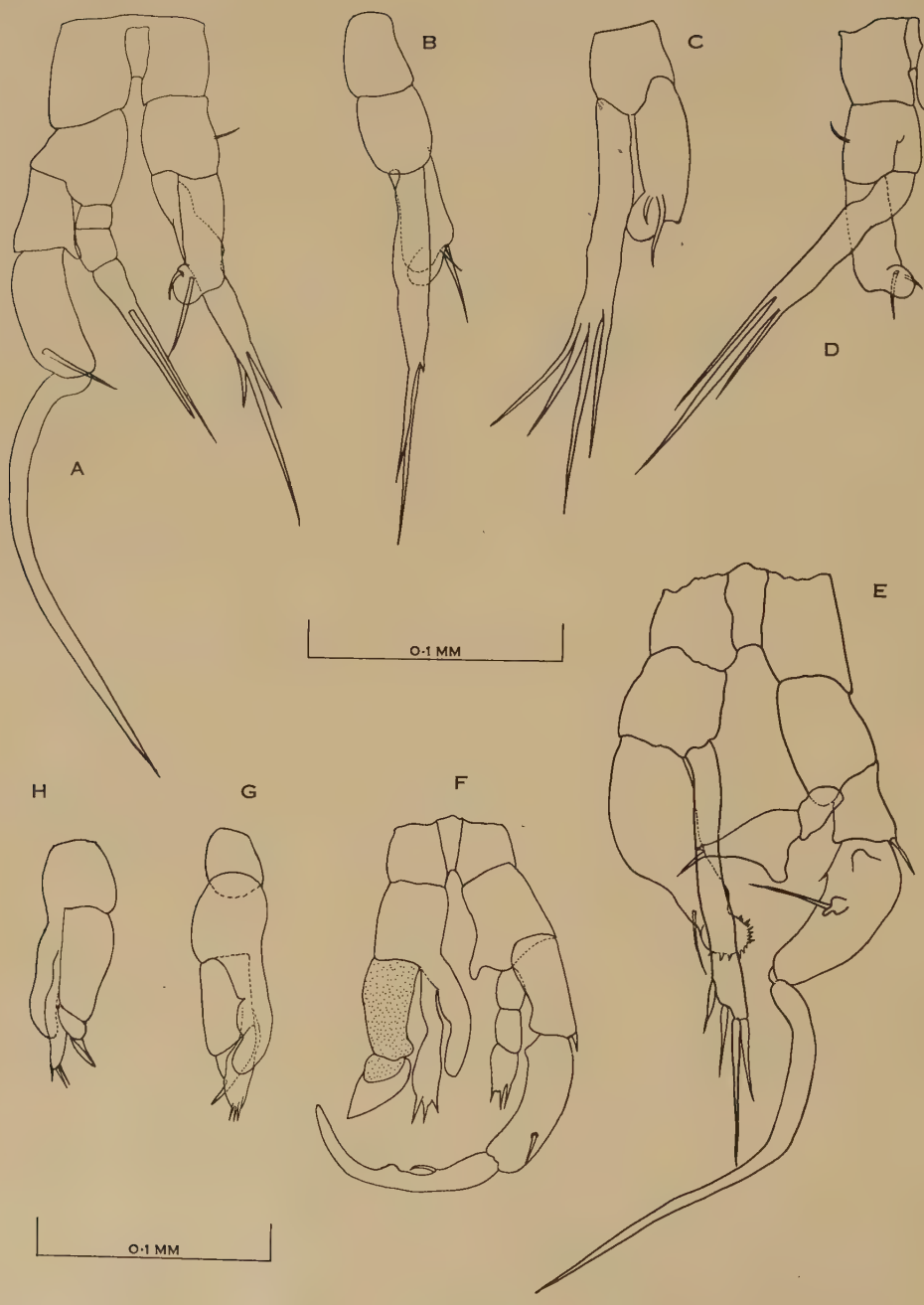


Fig. 1.—Male fifth legs. *A–D, Calamoecia lucasi* Brady: *A*, anterior aspect; *B–D*, various aspects of the left leg. *E, C. ampulla* (Searle), posterior aspect. *F–H, C. trifida*, sp. nov.: *F*, posterior aspect; *G–H*, different aspects of left leg.

description of *Brunella* proposed by Fairbridge (1945*b*) also provides a substantially correct definition of the genus *Calamoecia*, and is largely incorporated, but enlarged upon, in the generic characters given below. An unnecessary feature of Fairbridge's generic description is the requirement that the male fifth left exopodite should have a terminal segment and that this should be "flattened".

Ringuelet (1958, p. 41) separates the family Boeckellidae Brehm from the Centropagidae Sars, 1902. The characters chosen to do this are such that a further (third) family would have to be erected to accommodate *Calamoecia* only. This is considered unjustified, nor is it proposed to unite *Calamoecia* and *Boeckella* together in the one family (on the basis of the structure of the exopodite of the male fifth right leg) distinct from the Centropagidae. The genus is therefore treated as belonging to the family Centropagidae Sars.

## Order CALANOIDA

### Family **CENTROPAGIDAE** Sars

### Genus CALAMOECIA Brady

*Calamoecia* Brady, 1906, p. 696. Sars, 1908, pp. 11–12. Jolly, 1955, p. 280.
*Brunella* Smith, 1909, p. 87. Sars, 1912, pp. 4–5. Fairbridge, 1945*b*, p. 67.

Type (by monotypy): *Calamoecia lucasi* Brady.

*Generic Characters*

Small Centropagidae in which the endopodites of the swimming legs are 1-segmented in the first pair, and 2-segmented in pairs 2–4; endopodites of female fifth pair of legs may be indistinctly segmented, usually 1- or 2-segmented, rarely 3-segmented; exopodite of male fifth right leg 3-segmented, the distal segment consisting of a long, strongly developed claw as in *Boeckella*; endopodite of male fifth right leg not extending past the distal extremity of middle right exopodite segment; exopodite of male fifth left leg relatively short, in comparison with right exopodite, and neglecting any terminal process is usually shorter than left endopodite, not more than 2-segmented, may terminate in a variety of processes but never in a long claw as in *Boeckella*; urosome 5-segmented in the male, in the female 3-segmented and bearing a prominent ventral bulge on the genital segment; non-geniculate antennules 25-segmented, geniculate antennules 22-segmented.

## III. The Species

*Number of Species*

Both Jolly (1955) and Brehm (1959) omit reference to *Calamoecia salina* (Nicholls, 1944). When this species is included together with *C. trifida*, sp. nov., described below, and the loss of four species by synonymy is allowed for, the genus is now represented by nine described species, one of which contains two subspecies. These are as follows: *C. lucasi* Brady, 1906; *C. australica* Sars, 1908; *C. tasmanica* (Smith, 1909); *C. australis* (Searle, 1911); *C. ampulla* (Searle, 1911); *C. salina* (Nicholls, 1944); *C. attenuata* (Fairbridge, 1945); *C. tasmanica subattenuata* (Fairbridge, 1945); *C. gibbosa* (Brehm, 1950); and *C. trifida*, sp. nov.

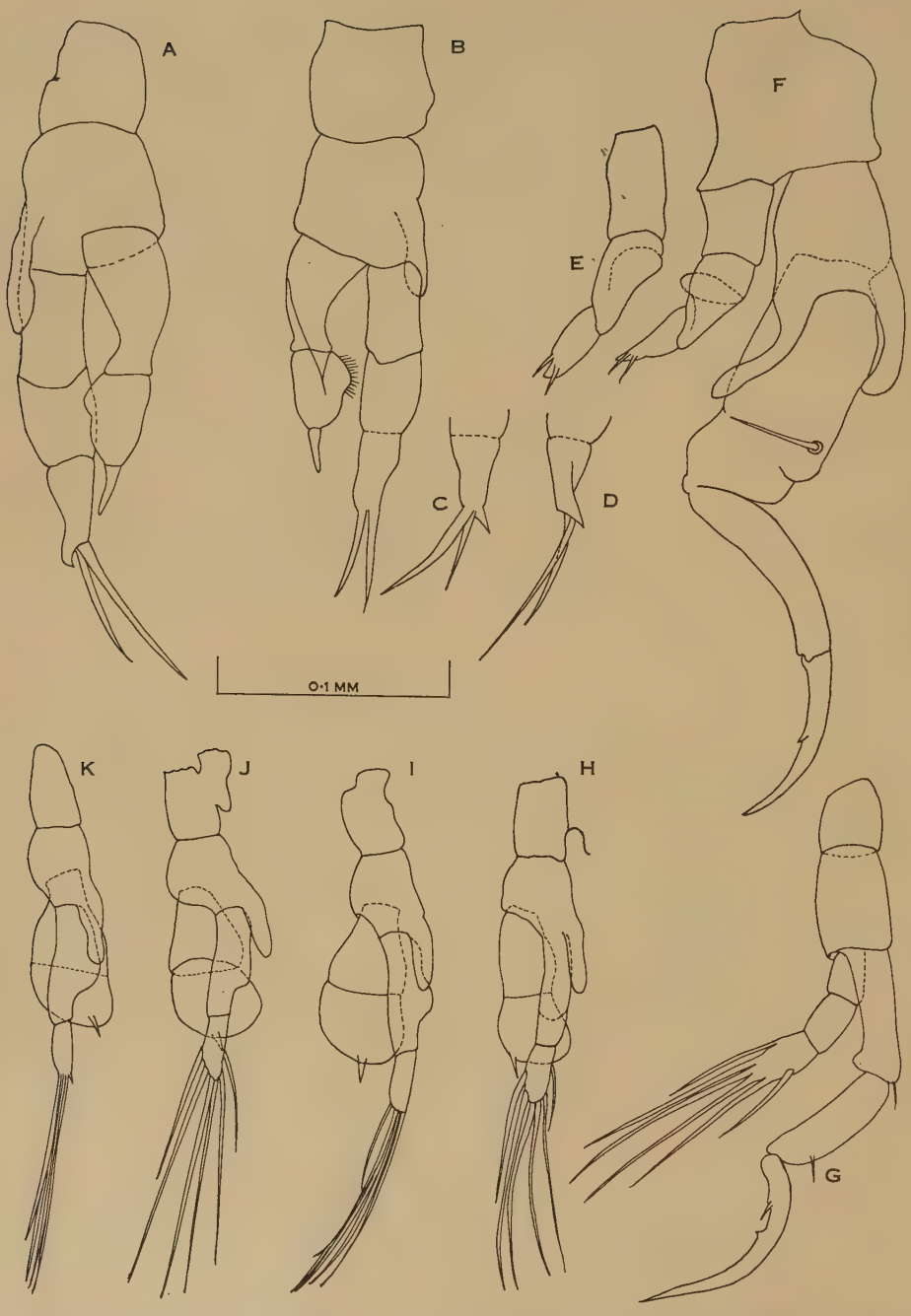


Fig. 2.—Male fifth legs. *A–F, Calamoecia salina* (Nicholls): *A–B*, anterior and posterior aspects respectively of left leg; *C–D*, different aspects of extremity of left endopodite; *E*, further aspect of right endopodite; *F*, posterior surface of right leg; *G–K, C. tasmanica tasmanica* (Smith): *G*, posterior surface of right leg; *H–K*, series of different aspects of left leg.

*Key to Species*

A key to both the males and females of all species listed above is given below. Generally the species are more easily identified from male specimens which usually are readily available. It will be noted that the segmentation of the endopodite of fifth feet, and the number of setae borne on it, have been avoided as important characters in the key to females. Both these features may be subject to variation within a species. It is strongly recommended that several specimens be examined when using the key to females.

### Key to the Males

(Based entirely on the structure of the male fifth legs)

1. Proximal segment right exopodite with 2 long curved processes arising from distal edge posteriorly ..... *C. salina* (Nicholls, 1944) (Fig. 2)
   Proximal segment right exopodite with straight distal edge posteriorly ..... 2
2(1). Right endopodite 1-segmented ..... *C. australica* Sars, 1908 (No figure)
   Right endopodite 2-segmented ..... 3
   Right endopodite 3-segmented ..... 4
3(2). Distal segment right endopodite with a pronounced outgrowth on the outer edge; left exopodite 1-segmented ..... *C. ampulla* (Searle, 1911) (Figs. 1 and 5)
   Distal segment right endopodite without any outgrowth on the outer edge; left exopodite 2-segmented ..... *C. australis* (Searle, 1911) (no figure)
4(2). Left exopodite distinctly 2 segmented, neglecting any terminal process or differentiations ..... 5
   Left exopodite 1-segmented but with terminal differentiation ..... 8
5(4). Distal segment left exopodite bearing spine(s) but not expanded terminally into a lamellar process ..... 6
   Distal segment left exopodite not bearing spine(s) but terminating in a thin, shovel-like expansion ..... *C. trifida*, sp. nov. (Fig. 1)
6(5). Left endopodite 2-segmented ..... 7
   Left endopodite 1-segmented ..... *C. gibbosa* (Brehm, 1950) (Fig. 5)
7(6). Distal segment left exopodite bearing a single spine ..... *C. tasmanica tasmanica* (Smith, 1909) (Figs. 2 and 5)
   Distal segment left exopodite bearing 2 spines (a large outer one and a much smaller inner one) ..... *C. tasmanica subattenuata* (Fairbridge, 1945) (Figs. 3 and 5)
8(4). Left exopodite produced at outer distal extremity into a serrated lamella, close to which is a single spine; left endopodite 2-segmented ..... *C. attenuata* (Fairbridge, 1945) (Fig. 3)
   Left exopodite differentiated at inner distal extremity into a rounded knob at the base of which arises a conspicuous spine, and frequently a second smaller spine; left endopodite 1-segmented ..... *C. lucasi* Brady, 1906 (Fig. 1)

### Key to the Females

("Exopodite" and "endopodite" refer to the fifth legs. Unless otherwise indicated these are illustrated in Figure 4. For key features not involving the fifth legs see Description of Species below)

1. Antennules extending backwards only as far as the posterior extremity of the metasome; distal exopodite segment typically with 2 straight spines of which the outer one is longer ..... *C. salina* (Nicholls, 1944)
   Antennules extending to the posterior extremity of the furcal rami or further; distal exopodite segment with more than 2 spines or, if only 2, then with the outer spine shorter than the inner one which is bent inwards ..... 2

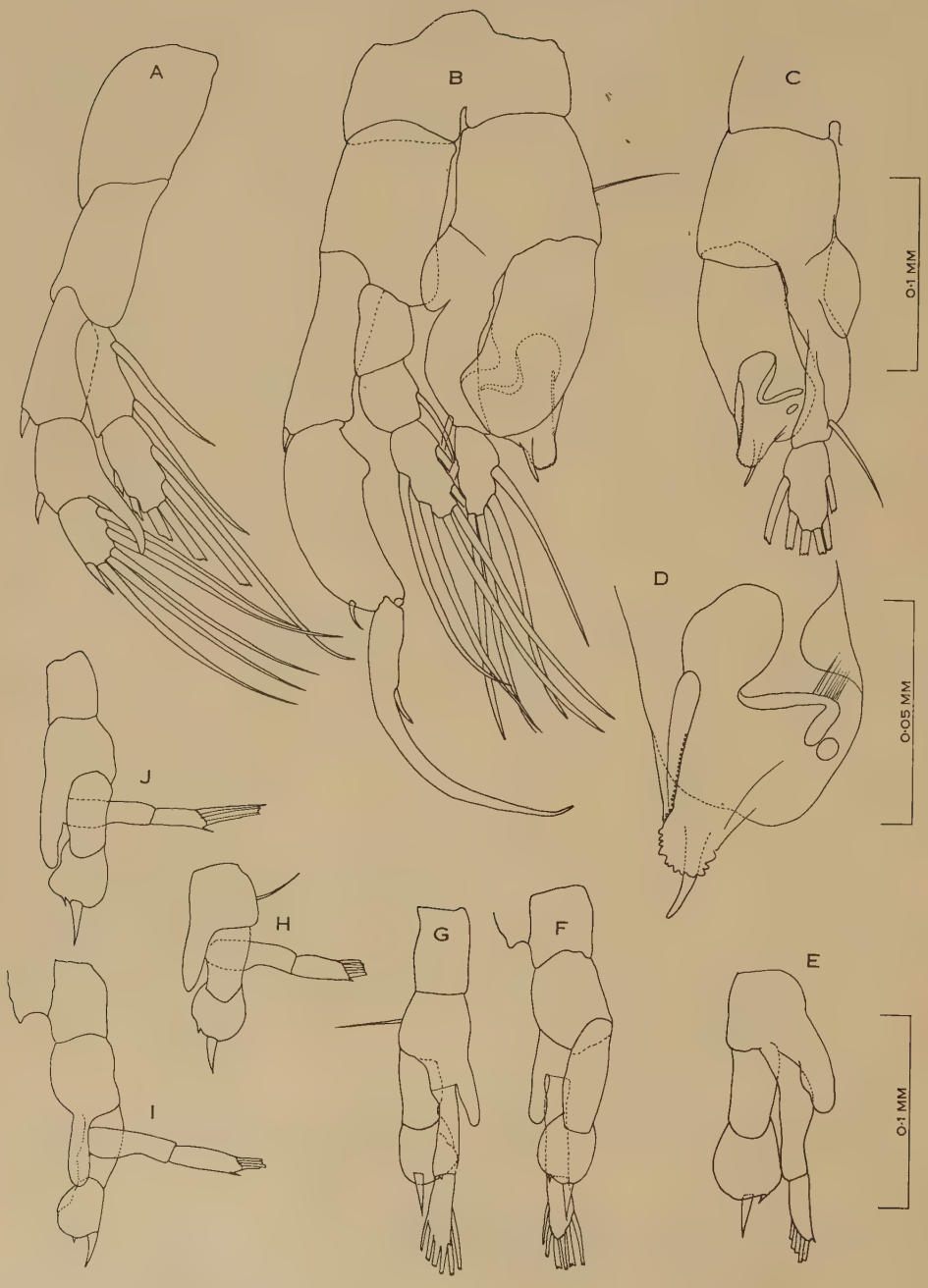


Fig. 3.—Male and female fifth legs. *A–D*, *Calamoecia attentuata* (Fairbridge): *A*, female; *B*, anterior aspect of male; *C*, posterior aspect of male left leg; *D*, extremity of *C*, showing detail. *E–J*, *C. tasmanica subattenuata* (Fairbridge): various aspects of left leg.

2(1). Distal exopodite segment with 2 spines; genital segment with a prominent lateral outgrowth on both sides ..... *C. gibbosa* (Brehm, 1950) (Fig. 5)

Distal exopodite segment with more than 2 spines; genital segment without a prominent lateral outgrowth on both sides ..... 3

3(2). Middle exopodite segment typically lacking an outer spine, maximum number of spines on terminal segment 4; maximum depth ventral bulge genital segment (viewed laterally) less than one-half depth of segment itself at posterior extremity; prominent process present on ventral aspect of genital segment posterior to bulge, this as long as bulge is deep ..... *C. trifida*, sp. nov.

Middle exopodite segment bearing an outer spine, maximum number of spines on terminal segment more than 4; maximum depth ventral bulge genital segment greater than one-half depth of segment itself at posterior extremity; any process present on ventral aspect of genital segment posterior to the bulge, short relative to bulge depth ..... 4

4(3). Fifth thoracic segment with rounded posterior extremities which do not extend into the posterior half of the genital segment ..... 5

Fifth thoracic segment with sharply pointed posterior extremities or wings which reach into the posterior half of the genital segment ..... 7

5(4). Terminal exopodite segment with rarely more than the typical 5 spines, but not uncommonly with fewer; of these, the spine immediately inside the outermost one is much longer than any of the others ..... *C. lucasi* Brady, 1906

Terminal exopodite segment almost invariably with 6 spines; of which the 4 closest to the short outermost one are subequally long ..... 6

6(5). Spine immediately adjacent to outermost one, on the distal exopodite segment, twice as thick at the base as any to the inside; average total body length less than 1·45 mm ..... *C. tasmanica* (Smith, 1909) (contains 2 subspecies separable in key to males)

Spines inside the outermost one of subequal thickness at the base; average total body length greater than 1·45 mm ..... *C. attenuata* (Fairbridge, 1945) (Fig. 3)

7(4). Wings of last thoracic segment tapering fairly symmetrically to a single point; endopodite typically unsegmented and with the terminal setae shorter than those on the inner edge ..... 8

Wings of last thoracic segment bifid, with a rounded lobe dorsal to the long sharp point; endopodite typically distinctly 2-segmented with terminal setae as long, or longer, than setae on the inner edge; (terminal exopodite segment with 6 spines one of which is easily the longest) ..... *C. australis* (Searle, 1911)

8(7). Distal exopodite segment typically with 5 spines ..... *C. ampulla* (Searle, 1911)

Distal exopodite segment typically with 6 spines (one of which is easily the longest) ..... *C. australica* Sars, 1908 (no figure)

*Description of Species*

The confusion of left and right fifth feet in the male as well as other errors made by Smith (1909) and Searle (1911, 1912) have been pointed out by Sars (1912), Henry (1924), and Nicholls (1944). This will not be dwelt upon further in descriptions of their species below.

The evaluation of some of Searle's species has been rendered difficult by the nature of the type material. In some cases females, rather than males, have been designated as type, the fifth legs have not been dissected off, and a non-permanent mountant has been used which in some cases has dried up and left the specimen distorted beyond recognition. In cases where it has been ascertained that the primary types have been lost or destroyed, topotypes have been secured for neotypes. Application will be made to the International Commission on Zoological Nomenclature for recognition of these neotypes. All type material has been deposited in the Australian Museum, Sydney.

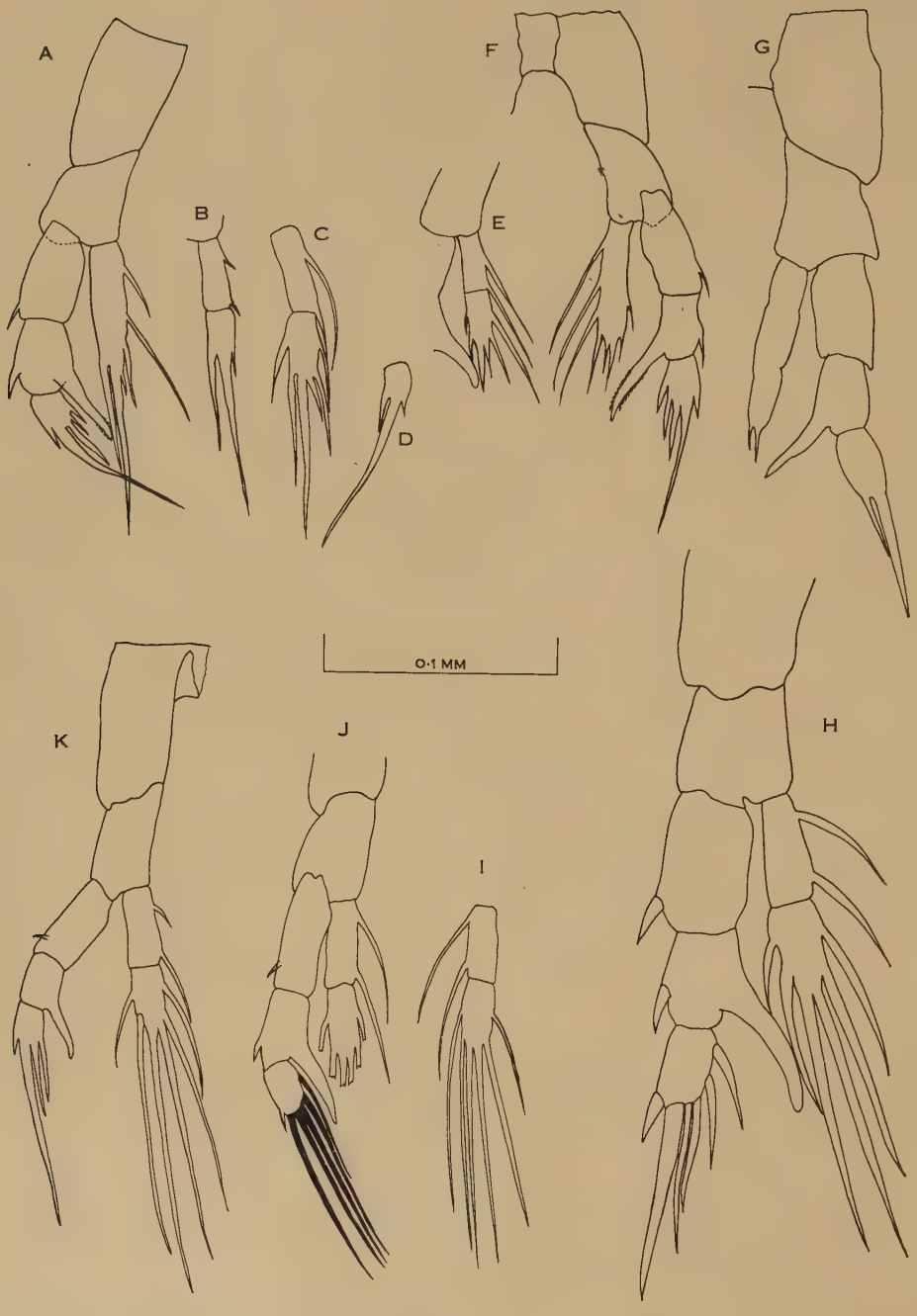


Fig. 4.—Female fifth legs. *A–D*, *Calamoecia lucasi* Brady: *A*, foot with 1-segmented endopodite; *B–C*, 2-segmented endopodites differing in spinosity; *D*, distal segment of exopodite with 3 spines. *E–F*, *C. ampulla* (Searle): *E*, 2-segmented endopodite; *F*, leg with 1-segmented endopodite. *G*, *C. salina* (Nicholls). *H*, *C. australis* (Searle). *I–J*, *C. tasmanica tasmanica* (Smith). *K*, *C. trifida*, sp. nov.

The nine species are dealt with in two groups as follows:

(1) The following species has not been encountered in field collections nor has it been possible to examine its type. At the same time it is a well-founded species according to its description, and there is no reason to doubt its existence. It is not figured, but is included in the key to species, and is listed below together with its type locality.

### Calamoecia australica Sars

*Calamoecia australica* Sars, 1908, pp. 12–14.

*Distribution*

VICTORIA: St. Arnaud.

(2) The remaining species have been encountered in field collections made during the present survey, or their type material has been examined, or both. All have been figured and where necessary described or redescribed. They are dealt with below in chronological order of description:

### Calamoecia lucasi Brady

Figs. 1*A–D*, 4*A–D*, 6*A–F*

*Calamoecia lucasi* Brady, 1906, pp. 696–7. Jolly, 1955, pp. 281–3.
*Brunella steeli* Henry, 1924, pp. 315–7.
*Limnocalanus lucasi* (Brady). Kiser, 1947, pp. 34, 36, figs. 6, 10 (partim, male only).
Non *Limnocalanus lucasi* (Brady). Kiser, 1947, pp. 34, 36, figs. 1–2 (partim, female only).

*Type*

Lakes Waikare and Roto-iti (Auckland, not Nelson); N.Z. British Museum (Natural History).

*Description*

In view of the number of contradictory statements and figures that have appeared concerning this, the type species of the genus, its vital taxonomic features are described in some detail below.

*Fifth legs.*—With regard to the structure of the male and female fifth feet, there are discrepancies in the descriptions between different authors, and even between the text and figures of the same author. This situation is summarized in Table 1 to which the present findings are appended.

(1) *New Zealand material.*—Female: Exopodite 3-segmented, proximal segment bearing a single short spine at outer extremity, middle segment bearing 2 spines—a long stout inner process and a single outer spine, distal segment terminating in usually 5 spines but number varying from 2 to 6 (2: 1%, 3: 16%, 4: 26%, 5: 56%, 6: 1%); endopodite usually 1-segmented but sometimes indistinctly or distinctly 2-segmented (1-segmented 91%, 2-segmented 9%), considered as a whole, bearing usually 5 setae but number varying from 1 to 7 (1: 1%, 2: 4%, 3: 5%, 4: 7%, 5: 33%, 6: 28%, 7: 22%).

Male: Left exopodite 1-segmented, terminating in an inwardly directed rounded knob (this not considered a segment), finely toothed around the edge, arising from base of knob usually a single conspicuous spine, but frequently an additional much smaller spine (1 spine 60%, 2 spines 40%); left endopodite considerably exceeding left exopodite in length, 1-segmented, terminating in usually

TABLE 1

STRUCTURE OF THE FIFTH PAIR OF FEET OF CALAMOECIA LUCASI

The first figure of the structural formulae gives the segmentation of the appendage, those following the oblique stroke give the number of setae or spines borne on each segment in the order proximal to distal. ? = no statement. N.Z. = New Zealand material (80 specimens each sex). A = Australian material (40 specimens each sex). Range or unusual condition indicated by brackets.

| Author | | Male | | | | Female | |
|---|---|---|---|---|---|---|---|
| | | Left | | Right | | Left and Right | |
| | | Endopod | Exopod | Endopod | Exopod | Endopod | Exopod |
| Brady (1906) | | | | | | | |
| | Fig. | 2/0:4 | 1/1 | 2/0:3 | 3/0:0:0 | 2/1:3 | 3/0:1:3 |
| | Text | 1/? | 1/1 | 2/? | ? | 2/? | 3/0:1:3 |
| Henry (1924) | | | | | | | |
| | Fig. | 3/0:0:3 | *3/0:0:1 | 3/0:0:3 | 3/0:0:0 | — | — |
| | Text | 2/0:? | *3/0:0:1 | 3/0:0:? | 3/? | 2/? | 3/?† |
| Kiser (1947) | | | | | | | |
| | Fig. | 1/4 | 1/1 | 3/0:0:3 | 3/0:1:0 | ‡ | ‡ |
| | Text | 1/? | 1/? | | 3/? | | |
| Jolly (1955) | | | | | | | |
| | Fig. | 1/4 | 1/1 | 3/0:0:2 | 2/1:0 | 2/2:4 | 3/1:2:3 |
| | Text | 1/4 | 1/1 | 3/0:0:2 | ? | 2(3)/(0):0:4 | ? |
| Present | N.Z. | 1/4(2–5) | 1/1(1–2) | 3/0:0:3(1–4) | 3/0:1(0–1):0 | 1(1–2)/5(1–7) | 3/1:2:5(2–6) |
| | A. | 1/4(3–5) | 1/1(1–2) | 3/0:0:4(2–4) | 3/0:1(0–1):0 | 1(1–2)/7(4–8) | 3/1:2:5(3–5) |

* Not 3-segmented in type examined.

† 3/0:2:4 in type.

‡ It is believed that the fifth legs of *Boeckella*, not *Calamoecia*, were examined and consequently formulae are omitted.

4 setae but number varying from 2 to 5 (2: 10%, 3: 28%, 4: 60%, 5: 3%); right exopodite 3-segmented, proximal segment and distal segment (the claw) spineless, middle segment usually with a single spine, rarely spineless (1 spine 93%, no spines 7%); right endopodite much shorter than right exopodite, 3-segmented, proximal and middle segment without spines or setae, distal segment bearing setae or setae

and spines—usually 3 but number varying from 1 to 4 (1: 1%, 2: 37%, 3: 40%, 4: 22%), these often of very unequal length.

(2) *Australian material.*—In general this agrees with the above description; details of the variability in the material are as follows:

Female: Spines distal segment exopodite, 3: 2%, 4: 19%, 5: 79%.
Endopodite segmentation, 1-segmented 82%, 2-segmented 18%.
Endopodite setae, 4: 2%, 5: 2%, 6: 15%, 7: 56%, 8: 25%.

Male: Left endopodite—setae, 3: 6%, 4: 54%, 5: 40%.
Left exopodite—spines, 1: 70%, 2: 30%.
Right exopodite—spines middle segment, 0: 6%, 1: 94%.
Right endopodite—spines distal segment, 2: 17%, 3: 35%, 4: 48%.

*Female fifth thoracic and genital segments.*—The posterior extremities of the fifth thoracic segment are rounded, and do not extend into the posterior half of the genital segment. The form of the ventral bulge on the latter appears to be quite important taxonomically, and has been largely overlooked in previous descriptions. Consequently the genital segment has been figured for this and all the remaining species. In *C. lucasi* the genital bulge is very pronounced and bears a characteristic pimple-like outgrowth on its posterior extremity.

*Discussion*

It is seen that this species is variable in the details of the spines or setae borne on certain segments of the fifth feet and in the segmentation of the female endopodites. However, in the male the segmentation is constant, and the structural features, particularly the form of the left exopodite, are highly characteristic of the species in all cases.

*C. lucasi* has not previously been recorded or described from Australia. However, it is seen that any differences between the Australian and New Zealand material relate to very minor points, and that in general the Australian material lies well within the range of variability exhibited by the New Zealand material. There seems therefore to be no question of the two specimen groups being taxonomically distinct even at the subspecific level.

The above percentages indicating overall variability in the two groups of material do not disclose the extent of variability from locality to locality within a group. This is considerable. Thus, for example, the population in Lake Pupuke, Auckland—the most peculiar of the eight New Zealand populations sampled—had the following modal figures for setation and spinulation of fifth feet; male left endopodite three, female distal segment exopodite three. Also in this population approximately 40% of the female fifth endopodites were distinctly or indistinctly 2-segmented. This condition, however, did appear occasionally in other populations.

It is important to point out that the degree of variability exhibited by *C. lucasi* in the number of spines on the terminal exopodite segment of the female fifth feet, is not true of all species of *Calamoecia*. Examination of an equal number of these feet of *C. tasmanica* from different populations did not reveal a single specimen in

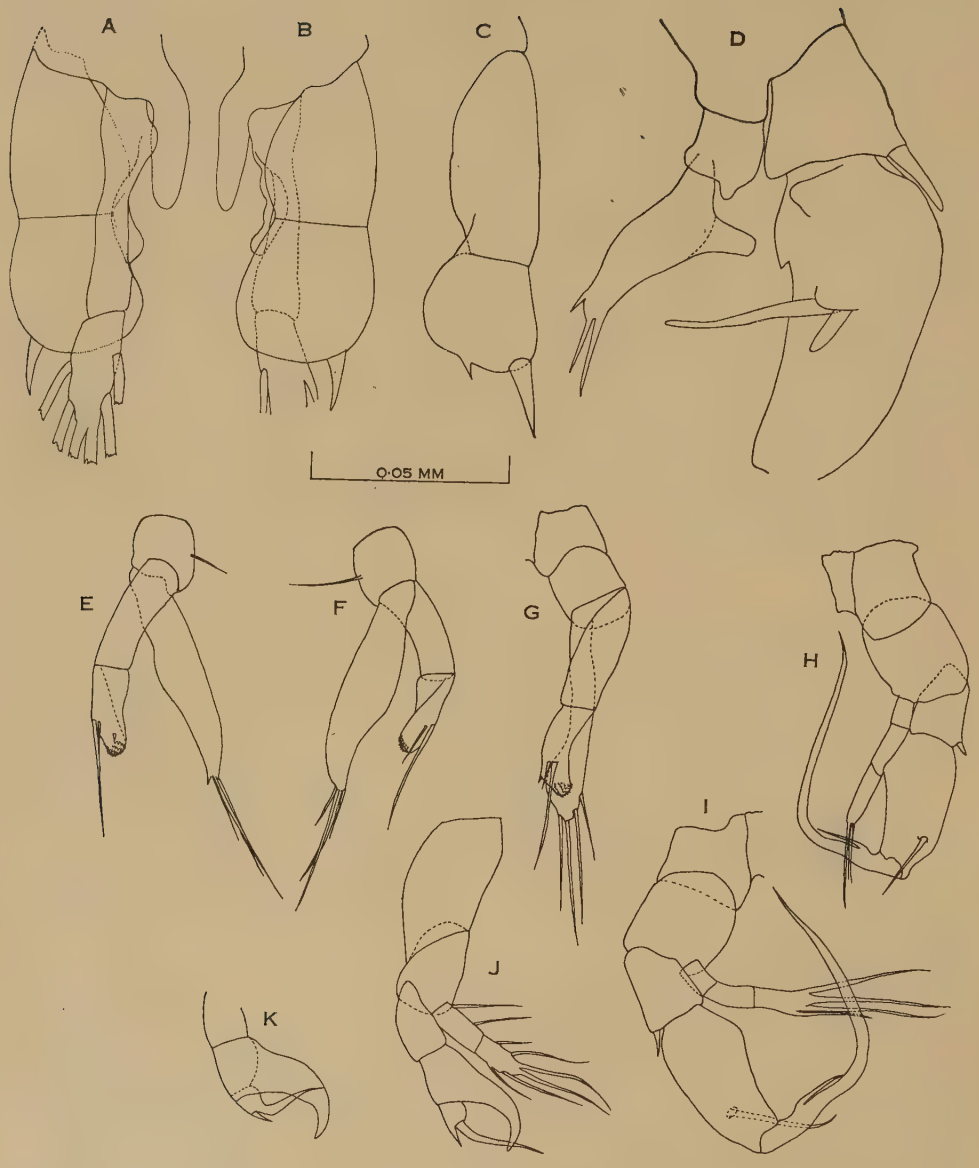


Fig. 5.—Male and female fifth legs. *A–B*, *Calamoecia tasmanica tasmanica* (Smith), ♂: *A*, posterior aspect of left leg; *B*, anterior aspect of left leg. *C*, *C. tasmanica subattenuata* (Fairbridge), ♂: anterior aspect of left exopodite. *D*, *C. ampulla* (Searle), ♂ from Western Australia: posterior aspect of endopodite and two segments of exopodite. *E–K*, *C. gibbosa* (Brehm): *E*, posterior aspect of ♂ left leg; *F*, anterior aspect of ♂ left leg; *G*, outer aspect of ♂ left leg; *H*, posterior aspect of ♂ right leg; *I*, anterior aspect of ♂ right leg; *J*, ♀ leg; *K*, exopodite ♀ leg, showing stronger than usual development of the inner process of the middle segment.

which the number of these spines varied from six. The number, shape, and relative size of these spines are important taxonomically.

Although the egg number was mentioned in previous specific descriptions, it is of no taxonomic value unless the time and locality of collections is also stated (Bayly 1959), and even then is of small significance. Up to 19 eggs have been observed in one egg sac. Egg number varies considerably in the one population at the one time (coefficient of variability of the order 20–30%), and the mean figure for the same population varies seasonally, being greater in the winter than in the summer. Furthermore there is a large variation in mean egg number in different lake populations even at the same time of the year when they are at approximately the same temperature (Table 2). Size (length) measurements show a similar pattern of variability.

TABLE 2

VARIATION IN EGG NUMBER OF CALAMOECIA LUCASI

Twenty-five specimens examined from each locality

| Date | Locality | Surface Temperature (°C) | Range | Mean | S.D. | Coefficient of Variability (%) |
|---|---|---|---|---|---|---|
| 31.xii.57 | Lake Rotokare, New Plymouth | 19·3 | 2–6 | 3·4 | 1·03 | 30 |
| 5. i.58 | Nowell's Lagoon, Hawera | 18·0 | 9–19 | 13·8 | 2·88 | 21 |
| 6. i.58 | Waipu Lagoon, New Plymouth | 18·5 | 4–10 | 7·0 | 1·66 | 24 |
| 22. iii.58 | Duck Creek, Auckland | 21·8 | 5–10 | 6·9 | 1·37 | 20 |

*Occurrence*

(1) *Previous* (New Zealand only).—AUCKLAND: Lake Waikare (Brady 1906; Jolly 1955); Lake Roto-iti (Brady 1906; Jolly 1955); Lake Tarawera (Kiser 1947; Jolly 1955); Lake Tikitapu (Kiser 1947); Lake Rotorua (Kiser 1947); Duck Creek, Chelsea (Henry 1924; Jolly 1955); Lake Pupuke, Takapuna (Henry 1924; Jolly 1955).

(2) *Present.*—NEW ZEALAND. AUCKLAND: Duck Creek, Chelsea; Lake Pupuke, Takapuna; Lake Waiharera, Far North; Swan Lake, Ngataki, Far North. TARANAKI: Lake Rotokare, New Plymouth; Waipou Lagoon, Bell Block, New Plymouth; Lake Rotokare, Eltham; Nowell's Lagoon, Hawera.

AUSTRALIA. QUEENSLAND: Cooby Reservoir, Toowoomba. NEW SOUTH WALES: University, Armidale; Lake Eucumbene, Adaminaby; Farm dam, Kempsey. VICTORIA: Lakes Kerford and Sambell, Beechworth. SOUTH AUSTRALIA: Hindmarsh Valley Reservoir; Thorndon Park Reservoir.

## Calamoecia tasmanica (Smith)

Figs. *2G–K*, *3E–J*, *4I–J*, *5A–C*, *7A–D*

*Brunella tasmanica* Smith, 1909, pp. 87–8. Searle, 1911, pp. 175–6. Brehm, 1953*a*, pp. 43–4.
*Brunella longicornis* Searle, 1912, pp. 196–7. Sars, 1912, pp. 5–9.
*Brunella subattenuata* Fairbridge, 1945*b*, pp. 69–70.
*Brunella* cf. *subattenuata* (Fairbridge). Brehm, 1953*b*, pp. 9–10.

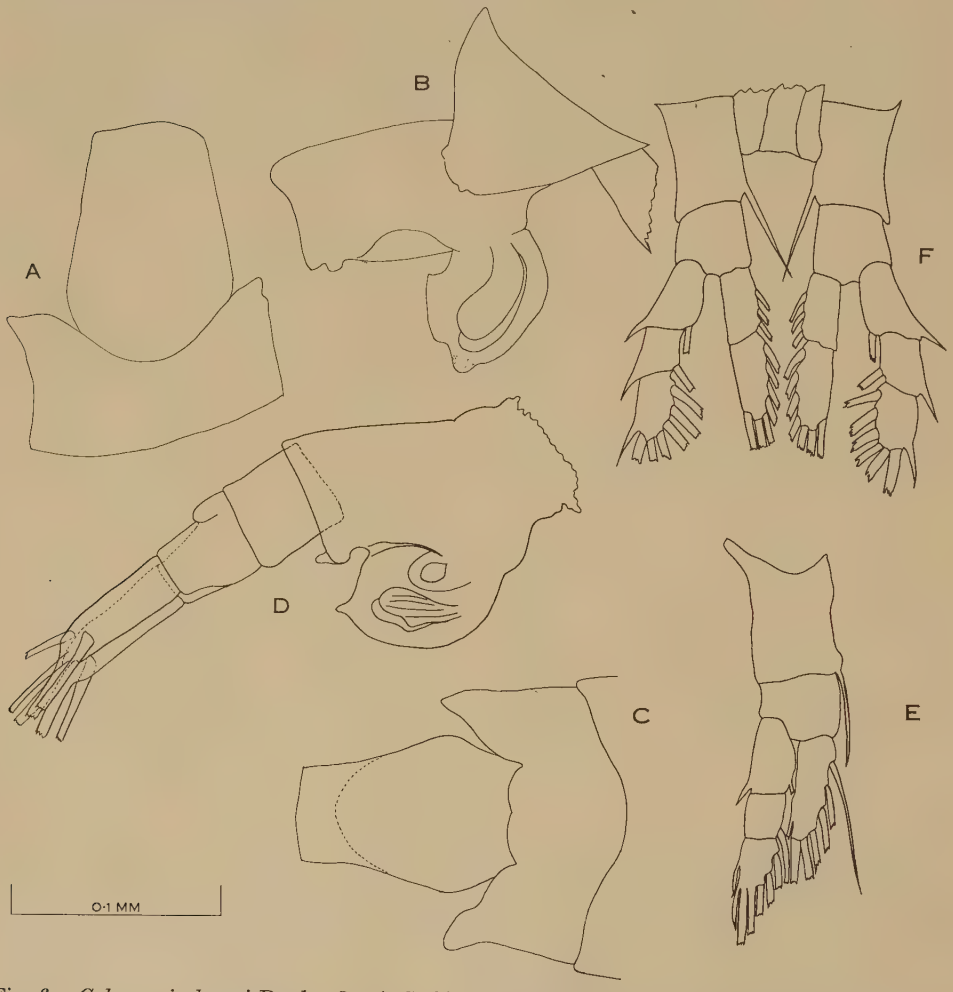


Fig. 6.—*Calamoecia lucasi* Brady, ♀. *A–C*, fifth thoracic and genital segments viewed dorsally, laterally, and dorsally (different specimen from *A*), respectively; *D*, lateral aspect of urosome; *E*, first swimming leg; *F*, second pair of swimming legs.

### *Discussion of Synonymy and Separation of Subspecies*

The similarities between the descriptions and figures of *C. tasmanica* and *C. longicornis* are more striking than the differences, and the criteria upon which they are separated are immediately suspect. Nicholls (1944) refers to the difficulty in separating these two "species".

Smith (1909) described *C. tasmanica* from Bruny Island, Tasmania. This species was subsequently recorded from Victoria by Searle (1911), who later (Searle 1912) described *C. longicornis* from a locality close to that where *C. tasmanica* was recorded. With regard to the structure of the fifth male legs *C. longicornis* was not distinguished by Searle, in the text, from *C. tasmanica*. His only statement concerning these structures was: "Fifth pair of legs in male closely resembling those of *B. tasmanica*, having the spatulate (left) exopodite and the peculiar lobes attached to the endopodite". His figure differs from that of Smith mainly in showing the proximal segment of the left endopodite with two basal lobes, in addition to possessing a shoulder marking the boundary between a thick proximal portion, and a thin distal portion. The endopod lobe shown by Smith (1909, pl. 18, fig. 16) can be equated to the boundary line between thick and thin portions, which in Searle's figure affects the outline of the inner edge (cf. Fig. 2*H* with Fig. 2*K*). The sole feature stressed by Searle in distinguishing *C. longicornis* from *C. tasmanica* was the length of the antennule relative to that of the body. Thus he stated that *C. longicornis* ". . . can be distinguished readily from other species by the great length of its first antennae" and that these antennae were ". . . of great length—far exceeding that of the whole animal, including the caudal setae . . ."—hence the specific name he chose. His figure (Searle 1912, pl. iii, fig. 1) shows an antennule length/body length ratio of 1·08 for one antennule and 1·00 for the other. Sars (1912) recorded *C. longicornis* from its type locality and gave it a much fuller description. It is noteworthy that his figure (Sars 1912, pl. vii, fig. 12) of the male fifth left leg agrees more closely with Smith's of *C. tasmanica* than Searle's of *C. longicornis*. This figure of Sars shows the proximal segment of the left endopodite with but one lobe—that shown by Smith—which is responsible for the proximal portion of this segment appearing much broader than the distal part when viewed from certain directions. It would appear, therefore, that Searle's figure is in error in showing two additional lobes. Like Searle, Sars made no verbal distinction between *C. longicornis* and *C. tasmanica* with regard to the male fifth legs, but rather stressed the similarity of these in the two species, stating that those of *C. longicornis* ". . . on the whole are built in a very similar manner to . . *tasmanica*". Sars remarked that *C. longicornis*, ". . . is closely allied to . . . *tasmanica* Smith, but is of smaller size and still more slender form of body, differing moreover in the greater length of the anterior antennae". However, it should be noted that Sars never recorded *C. tasmanica* and therefore presumably never distinguished specimens of it from *C. longicornis*. Thus his above remarks concerning the length of the antennule relative to that of the body would have been formulated by a comparison of a topotype of *C. longicornis* with Smith's description and figures of *tasmanica*. His figures (Sars, 1912, pl. ii, figs. 1 and 2) show an antennule length/body length ratio of 1·01. Sars's remaining distinctions—those relating to size and body form—amount to little, and the statement concerning size is apparently without foundation in any case, since Smith records the length of *C. tasmanica* females as 0·7 mm while Searle and Sars record a length of 1·5 mm and "about 1 mm" respectively for *C. longicornis*. Brehm (1953*a*) recorded *C. tasmanica* from Tasmania and figured the male fifth legs but made no statement concerning relative antennule length. His figures of the male fifth legs are essentially similar to those of Sars (1912) for *C. longicornis*.

From the above arguments it is submitted that with regard to the published descriptions of *C. longicornis* and *C. tasmanica* the fifth legs of male specimens are indistinguishable and that the only difference between the two nomina lies in the length

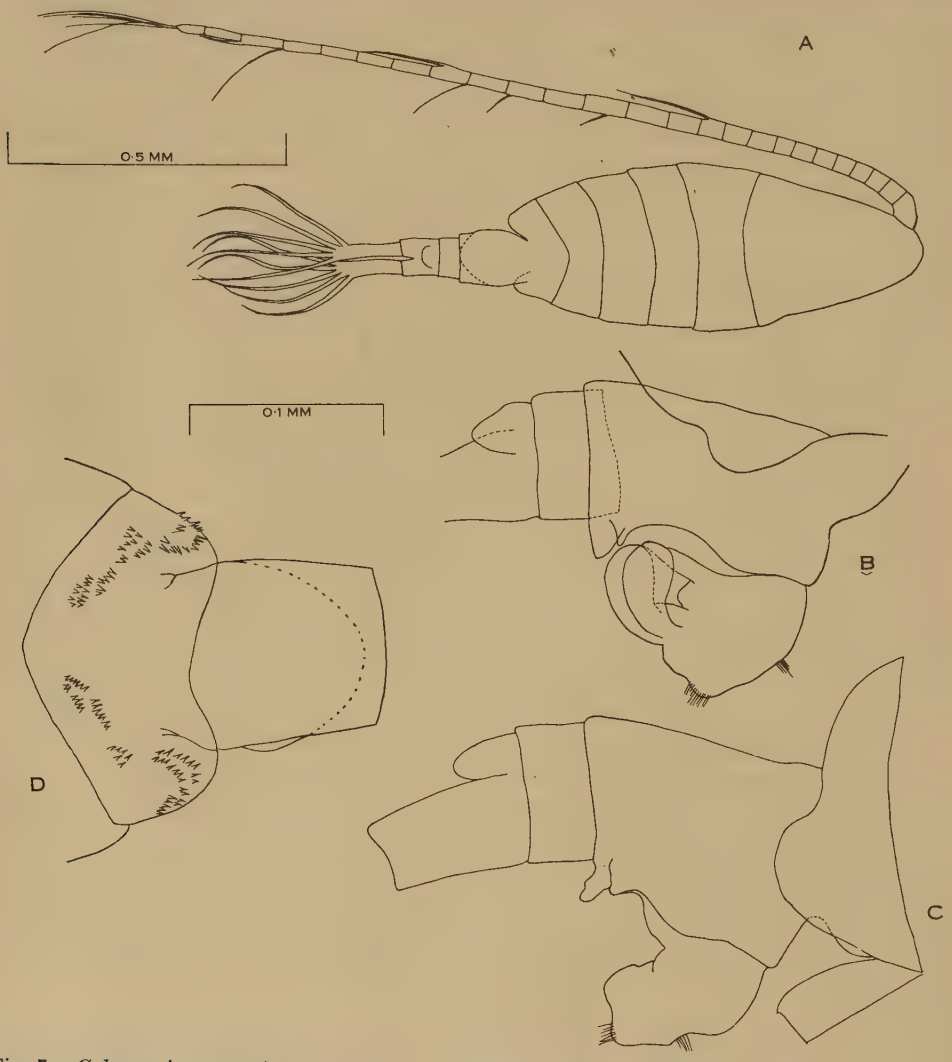


Fig. 7.—*Calamoecia tasmanica* (Smith), ♀. *A*, dorsal view, showing length of antennule relative to that of the body; *B–C*, lateral view of fifth thoracic segment and urosome, *B* showing extrusion of internal bulbs from ventral bulge; *D*, dorsal aspect of fifth thoracic and genital segments of variant from Lake Cooloolah.

of the non-geniculate antennules relative to the body in mature specimens. From general considerations it would seem most unlikely that two "good species" would correspond with these two nomina.

Searle alone has claimed to be able to separate *C. longicornis* specimens from *C. tasmanica* specimens. An examination of his type of *C. longicornis* and other

material lodged in the National Museum of Victoria has disclosed that:

(1) The antennule of the *C. longicornis* type (female holotype) is only very slightly longer than the total body length inclusive of the furcal setae (ratio 1·01), and is no longer than a specimen identified by him as *C. tasmanica* (ratio 1·01).

(2) In a female topotype of *C. longicornis* the ratio was 0·96.

(3) The male fifth legs of specimens identified by him as *C. longicornis* are identical with those of specimens identified by him as *C. tasmanica*.

Extensive enquires have failed to locate any primary types for *C. tasmanica*, but topotypes of *C. tasmanica* from Adventure Bay, Bruny Island, Tasmania, have been examined. In these the antennule length/body length ratio for females is 0·94 (average for 10 specimens) which is not considered significantly less than the ratios for Searle's *C. longicornis* material. The male fifth feet of *C. tasmanica* topotypes are identical with those of the latter group. Thus *C. longicornis* is declared synonymous with *C. tasmanica*. Smith (1909, pl. 18, fig. 6) is either slightly in error in showing the antennule extending only as far as the posterior limit of the furcal rami (ratio 0·86) or else figures a variant. The antennule length/body length ratio has been measured in 10 female specimens from each of two Queensland localities and the averages obtained were 0·97 and 0·93.

It is doubtful whether adequate criteria exist for separating *C. subattenuata* from *C. tasmanica* at the specific level. Fairbridge (1945*b*) described *subattenuata* from West Australia and noted that "this species resembles *B. longicornis* Searle (1912), but from Searle's description appears to be distinct in a number of points in the male fifth leg, and also in the length of the female caudal rami". It thus appears that Fairbridge limited the comparison of his form to Searle's description of *C. longicornis*, and did not consider its relationship to Sars's (1912) redescription of *C. longicornis*, or to *C. tasmanica*. However, when Fairbridge's figures of the male fifth feet of *C. subattenuata* are compared with *C. tasmanica* topotypes or Sars's figures of *C. longicornis*, certain differences in the left foot are still apparent. Examination of *C. subattenuata* topotypes confirms the essential accuracy of Fairbridge's figures and establishes these differences as real ones. The only feature in which the topotypes significantly differ from Fairbridge's figures of the male fifth left foot is in the absence of anything corresponding well with the blunt process shown on the proximal outer edge of the distal exopodite segment (Fairbridge 1945*b*, pl. iii, fig. 9). The male fifth left foot of *C. subattenuata* differs from that of *C. tasmanica* in the following respects:

(1) The distal exopodite segment bears two spines instead of one. The larger spine is longer relative to the distal segment than is the single spine in *C. tasmanica*, and in addition there is a much smaller spine to the inside.

(2) The two exopodite segments are less equal in length than they are in *C. tasmanica*, the proximal segment being distinctly the longer. The shapes of both these segments differ somewhat in the two forms.

(3) The shoulder on the proximal half of the proximal endopodite segment is less well developed and is of less complex structure than in *C. tasmanica*.

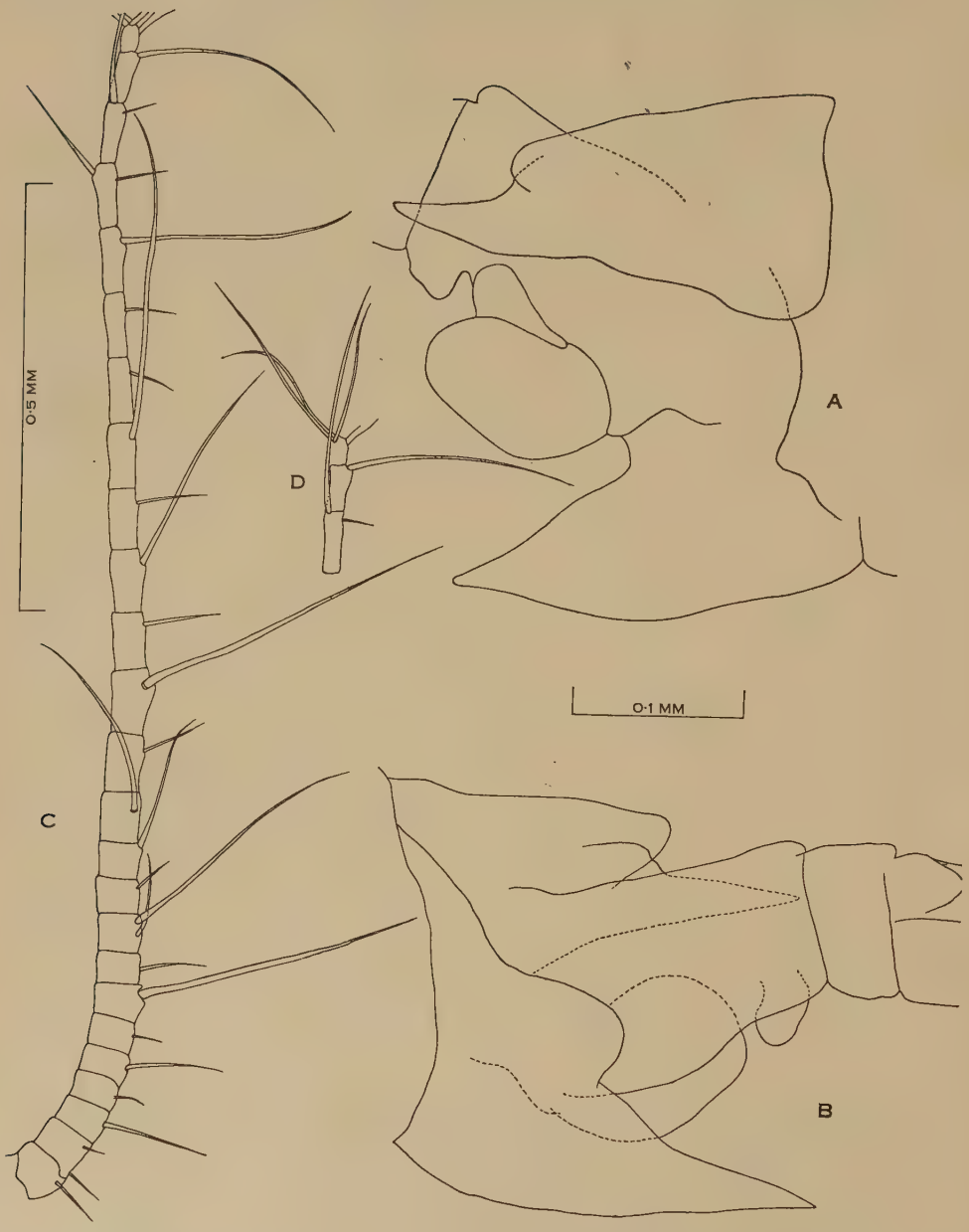


Fig. 8.—*Calamoecia australis* (Searle), ♀ (syntypes). *A*, ventrolateral aspect of fifth thoracic and genital segments of first syntype; *B*, dorsolateral aspect of fifth thoracic and genital segments of second syntype; *C*, dorsal aspect of antennule; *D*, distal segments of antennule.

It has yet to be determined whether these morphological differences are sufficient to isolate *C. subattenuata* reproductively from *C. tasmanica*, but it is considered that the two forms exhibit a lesser degree of morphological differentiation than that observed between the remaining species. For this reason *C. subattenuata* is given subspecific, rather than specific status. In support of this action it is pointed out that except for the above differences, the male fifth feet of the two forms agree closely. The right legs are indistinguishable, while both possess the same prominent inner protopodite process on the left leg, and show differentiation of the proximal segment of the left endopodite into thick and thin portions. Further, the author is unable to make a satisfactory distinction between *C. subattenuata* and *C. tasmanica* with respect to female specimens. The female fifth feet of *C. subattenuata* agree exactly with *C. tasmanica* and differ from the majority of other species in possessing six spines on the distal exopodite segment, four of which are subequal in length. There do not appear to be any significant differences between the female caudal rami as suggested by Fairbridge. In both forms the caudal rami vary from less than four to more than five times as long as the proximal width. Finally, the two forms are ecologically similar in that the majority of records for both are from localities relatively close to the sea.

### Calamoecia tasmanica tasmanica (Smith)

Figs. 2*G–K*, 4*I–J*, 5*A–B*, 7*A–D*

Topotypes 13♂♂, 7♀♀, Aust. Mus. Reg. No. P13495.

*Description*

*C. tasmanica tasmanica* has been given an adequate general description by Sars (1912) and the structure of the male fifth feet has been dealt with in the above discussion. It will therefore suffice to mention only the following few points to supplement the above figures.

*Fifth legs.*—(1) Male: The shape of the exopodite of the left leg has been described incorrectly by both Smith (1909) and Searle (1911, 1912) as being "spatulate" or "flattened". As seen from Figure 2*H–K* and as described by Sars (1912) this ramus is club-shaped and is approximately circular in cross section without any pronounced flattening. The distal segment is roughly globular.

(2) Female: The distal segment of the exopodites usually bears a total of 6 spines. There is a short outer spine inside which are 5 long ones, the 4 most distal of which can be described as being of subequal length. Certainly the 3 or 4 spines closest to the short outer one are more equal in length than the corresponding ones, where they exist, in the other species.

*Female fifth thoracic and genital segments.*—*C. tasmanica* belongs to the group of species in which the posterior extremities of the fifth thoracic segment are not sharply pointed. The genital bulge is very pronounced and is frequently observed with the two internal bulbs extruded. Usually the bulge bears two patches of fine setae—one at the posterior extremity and one ventrally.

*Variation*

All females examined from Lake Cooloolah, Queensland, differed from those of all other populations sampled in possessing a series of spines on the dorsolateral aspects of the fifth thoracic segment (Fig. 7*D*). In all other respects these females appeared to conform with those of other populations as did the males in which the fifth feet showed no divergence from the normal condition.

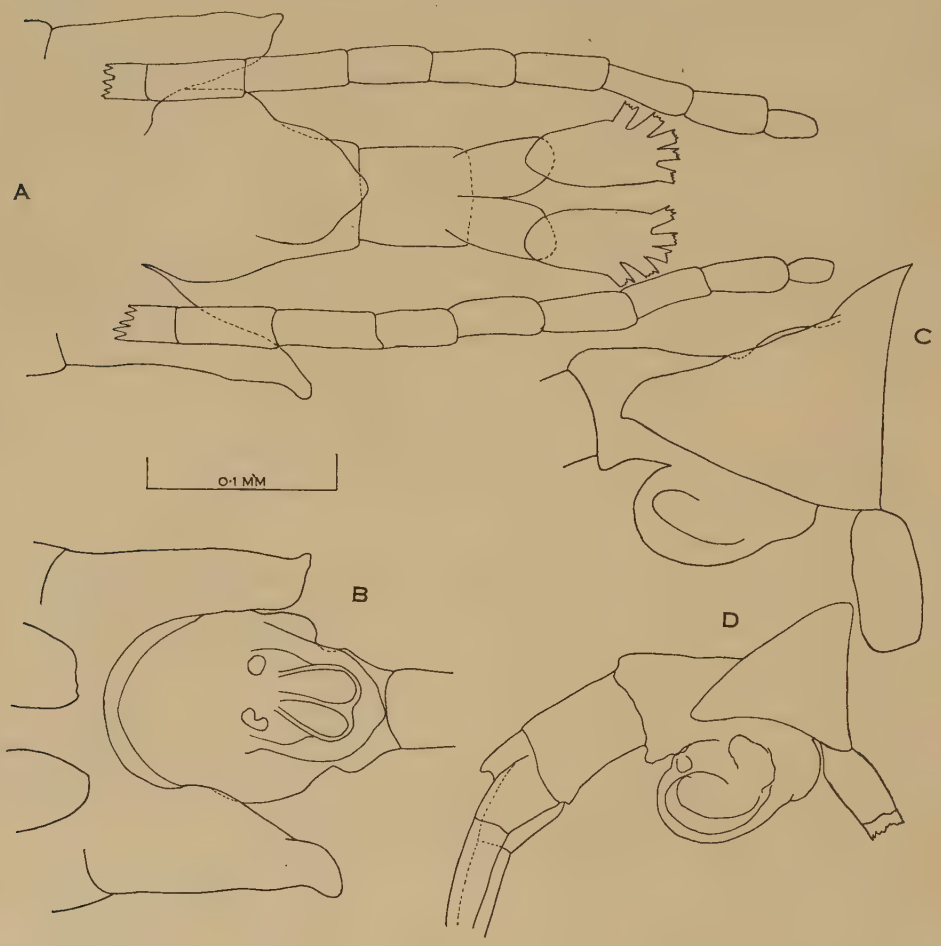


Fig. 9.—*Calamoecia ampulla* (Searle), ♀. *A*, ventral view of fifth thoracic segment, urosome, and distal segments of antennules; *B*, ventral view of fifth thoracic and genital segments, with internals of genital bulge shown; *C*, lateral aspect of fifth thoracic and genital segments; *D*, lateral aspect of fifth thoracic segment and urosome.

*Occurrence*

(1) *Previous.*—TASMANIA: Bruny Island (Smith 1909), Big Lake Waterhouse (Brehm 1953*a*). VICTORIA: Nyora and Caulfield (Sars 1912; Searle 1912), Cheltenham (Searle 1911).

(2) *Present.*—TASMANIA: Bruny Island, Big Lake Waterhouse. QUEENSLAND: Lake Karboora, North Stradbroke Island; Lake Cooloolah, Noosa. VICTORIA: Swamp near Fernbank, West Gippsland.

### CALAMOECIA TASMANICA SUBATTENUATA (Fairbridge), comb. nov.

Figs. 3*E–J*, 5*C*

Topotypes 6♂♂, 7♀♀, Aust. Mus. Reg. No. P13496.

*Description*

The features distinguishing this form from *C. tasmanica tasmanica* (Smith) are mentioned above and the structure of the male fifth left foot of topotypes is shown in the figures. Once again the terminal exopodite segment of this foot has been described as being "flattened", but this description of Fairbridge's is contradicted by his figures (Fairbridge 1954*b*, pl. iii, figs. 9 and 10) and by topotypes which show it to be approximately spherical.

*Occurrence*

(1) *Previous.*—WEST AUSTRALIA: Albany, Porongorups, and Perth (Fairbridge 1945*b*); Denmark and Greenbushes (Brehm 1953*b*).

(2) *Present.*—WEST AUSTRALIA: North Lake, Fremantle; University and Canningvale, Perth.

### CALAMOECIA AUSTRALIS (Searle)

Figs. 4*H*, 8*A–D*

*Brunella australis* Searle, 1911, pp. 176–7.
*Brunella viridis* Searle, 1911, pp. 177.
*Brunella expansa* Sars, 1912, pp. 9–10. Brehm, 1953*a*, pp. 44–5 (excluding fig. 26?).

Types: Nyora, Vic.; National Museum of Victoria.

*Discussion of Synonymy and Specific Diagnosis*

This species has not been encountered in any collections made during the present survey. In addition to Searle's original description, two female syntypes are the only material available for a decision on the validity of *C. australis* and a description of its diagnostic features. These have been examined in detail and the figures prepared from them. There appears to be little doubt that the specimen from which Figure 8*A* was drawn was the one illustrated by Searle (1911, pl. xii, fig. 1)—it is orientated on the microslide in a closely similar manner to that shown in Searle's figure, and is quite differently positioned from the second type shown in Figure 8*B*. Examination confirms that these syntypes are specimens of the same species and further that this species is clearly differentiated, even in the female, from *C. lucasi*, *C. australica*, and *C. tasmanica*, which were the only previously described species. There seems, therefore, no reason to doubt the validity of the species. The following features appear to be of value in propounding a differential diagnosis of its females:

(1) The fifth thoracic segment is sharply pointed at its posterior extremities. As shown in Figure 8*A–B*, this segment is produced posteriorly into two lobes—a small rounded one dorsally and a long pointed one ventrally. The latter one reaches almost to the posterior extremity of the genital segment.

(2) The fifth feet possess a stout outer spine on each of the exopodite segments, the distal one of which bears a total of 6 spines, of which the four closest to the outer one are not subequal in length. Searle's (1911, pl. xii, fig. 7) drawing of these feet disagrees in several respects with the material he designated as type.

(3) The number, relative lengths, and distribution of the spines and setae on the antennules are as shown in Figure 8*C–D*. All four antennules were examined and all agree with this figure.

If females possessing the above features can be assigned to this species with reasonable confidence, then an examination of the accompanying males will enable Searle's description of the male to be verified or corrected. With regard to (1) and (2) above, the females of *C. expansa* as described by Sars (1912, pl. viii, figs. 1–3) agree perfectly with the *C. australis* types. Concerning (3) it is unlikely that Sars intended his drawing of the antennule of *C. expansa* to have any important taxonomic value, nevertheless there is considerable agreement between it and Figure 8*C–D*, if correspondence of long setae is examined. It is considered that the close agreement between Sars's (1912) description of the female of *C. expansa* and Searle's *C. australis* types, together with the fact that the two were collected at almost exactly the same time of the year from precisely the same type locality, provide sufficient grounds for declaring *C. expansa* and *C. australis* synonymous. There is nothing basically incompatible between Searle's and Sars's figures of the male fifth feet, on the contrary there are points of agreement to support the synonymy. Most importantly the left exopodite of both *C. australis* and *C. viridis* is shown to consist of two segments of which the distal one is the smaller, and is differentiated into a solid smooth portion, and a distal tongue-shaped portion beset with minute spines. The main difference is that *C. australis* is shown with the tongue-shaped portion pointing along the long axis of the exopodite, whereas in *C. expansa* it points inwards almost at right angles to the long axis. The condition shown for *C. australis* would be produced by rotation of the tongue from its normal inwardly directed position. That this is the normal position is indicated by the agreement of Searle's (1911) figure of *C. viridis* (see below) and Brehm's (1953*a*) with Sars's of *C. expansa*. A further point of agreement between the figures of the male fifth feet of *C. australis* and *C. expansa* is the 2-segmented right endopodite. The disagreement in the segmentation of the left endopodite in these same figures is considered relatively unimportant.

As for the relationship between *C. viridis* and *C. expansa*, the male holotype of *C. viridis* is so badly damaged and distorted that an examination of the important taxonomic features is impossible. However, with regard to the male fifth feet, there is a striking correspondence between Searle's (1911, pl. xiii, figs. 2 and 3) figures of *C. viridis* and Sars's (1912, pl. viii, fig. 4) figures of *C. expansa*. Except that Searle shows an anterior view, whereas Sars shows a posterior view, there is almost perfect

correspondence between their figures of the left exopodite. This ramus is the most important single taxonomic feature and it is possible to identify all species of *Calamoecia* on the basis of its structure alone. There is thus little doubt that these nomina are synonymous. The most noticeable difference between the above figures is that Searle shows the left endopodite to be 2-segmented whereas in Sars's figure it is 1-segmented. It could be that in this respect Searle's figure is in error, but it is not impossible that the segmentation is subject to variation. In all events this discrepancy is not of prime importance, and does not seriously detract from the good agreement of the left exopodites. With regard to agreement between the females of *C. viridis* and *C. expansa*, the fifth thoracic segments of both are shown with pointed posterior extremities which reach almost to the posterior extremity of the genital segment. A smaller rounded lobe dorsal to the pointed lobe on each side is shown for *C. expansa* (Sars 1912, pl. viii, figs. 1 and 2) and the same condition is hinted at on the right side of Searle's (1911, pl. xiii, fig. 1) figure. There is approximate agreement between the figures of the female fifth feet of *C. viridis* and *C. expansa* —the distal segment of the exopodite of both is shown with six spines, although the outer one of *C. viridis* is disproportionately long. The only material of *C. viridis*, apart from the damaged holotype, among Searle's slide material lodged in the National Museum of Victoria is a female topotype. The fifth feet of this agree almost exactly with those of *C. expansa* and the *C. australis* syntypes.

To summarize, it is considered that adequate grounds exist to declare *C. australis*, *C. viridis*, and *C. expansa* synonymous. *C. australis* and *C. viridis* take date precedence over *C. expansa*, and *C. australis* takes page precedence over *C. viridis*.

Brehm (1953*a*) points out differences in the form he records from Sars's description of *C. expansa*, but he does not mention that the endopodite of the male fifth right leg is 3-segmented—which is the condition shown in his figure—whereas it is 2-segmented in Sars's description.

One of the following possibilities may explain this discrepancy:

(1) This endopodite is variable in segmentation. It does not, however, appear to be variable in other species, although the endopodites of the female fifth feet do vary in segmentation in the one species.

(2) Brehm's form was not *C. expansa* but a new species. The other differences listed by Brehm, especially those involving the female fifth feet, give credence to this possibility. The present author finds difficulty in identifying the female fifth legs described by Brehm with those of *C. australis*. The form and number of spines on the terminal segment of the exopodite are important taxonomically, and in Brehm's (1953*a*, fig. 26) figure these do not agree with those of *C. australis*. The possibility cannot be overlooked that the female fifth feet illustrated by Brehm belong to a different species to the male described. Alternatively an atypical specimen may have been figured. However, except that Brehm does not show the six endopodite setae, there is good agreement between Sars's and Brehm's figure of the male fifth left leg, so that the male does appear to have been correctly assigned to *C. expansa*.

(3) Sars's figures and text are in error.

(4) Brehm's figure is incorrect.

Which of these is correct, cannot yet be decided with certainty. It is suggested that (4) is the most likely, since Brehm (1953*a*, p. 44) stated that the form he examined was compared with Sars's figures, and the 3-segmented condition of the endopodite was not mentioned as a feature in which the form differed from Sars's description. *C. australis* is thus considered to have this endopodite 2-segmented, as described by Sars and Searle, and is placed in the key accordingly.

*Occurrence*

TASMANIA: Big Lake Waterhouse (Brehm 1953*a*). VICTORIA: Nyora (Searle 1911; Sars 1912); Heidelberg, Melbourne (Searle 1911).

### CALAMOECIA AMPULLA (Searle)

Figs. 1*E*, 4*E–F*, 5*D*, 9*A–D*

*Brunella ampulla* Searle, 1911, pp. 177–8.

Proposed neotype: ♂, Aust. Mus. Reg. No. P13493; topotypes 4♂♂, 2♀♀, Aust. Mus. Reg. No. P13494.

Material from several lakes in Victoria, South Australia, and Western Australia yielded a species which differs slightly from Searle's (1911) description of *C. ampulla*, but agrees exactly with topotypes, and is doubtlessly that species. The male fifth legs differ from Searle's drawing in but a single important point mentioned below. Examination of topotypes, including one collected and identified by Searle himself as *C. ampulla*, indicates that with regard to this point Searle's figure and text are in error. The holotype (male) itself is damaged and does not permit an examination of the fifth legs.

*Description of Female*

*Cephalothorax.*—There are the usual 5 free thoracic segments, not 4 as shown by Searle. The last thoracic segment has pointed posterior extremities.

*Abdomen.*—The genital segment has a very pronounced, bulbous, ventral bulge as in *C. lucasi* but without the prominent posterior point on the bulge of that species.

*Fifth legs.*—The exopodites are essentially as shown by Searle. The endopodites are usually 1-segmented as figured by Searle, and bear usually 8 setae, the terminal ones of which are shorter than those on the inner edge. The endopodites may, however, be 2-segmented as shown in Figure 4*E*.

*Description of Male*

*Fifth legs.*—The left leg agrees almost precisely with that labelled by Searle as the right, and is somewhat reminiscent of the left leg of *C. lucasi*. The left exopodite is 1-segmented and very stout over the proximal half beyond which it narrows suddenly and bends slightly inwards. At its distal extremity it is differentiated into a rounded knob, toothed around its edges. Near the base of this knob, on the outer edge, arises a single spine. The left endopodite is long, 1-segmented, and terminates in usually 4 spines (sometimes 3).

The right exopodite shows the usual 3-segmented condition and terminates in the usual claw. The proximal segment bears a single outer spine. The posterior surface of the middle segment bears a raised knob close to its proximal margin, while midway along its length there arises from a second knob a long inwardly pointing spine, and close to its base a second much shorter spine. On the inner proximal edge of this segment is located a single small tooth.

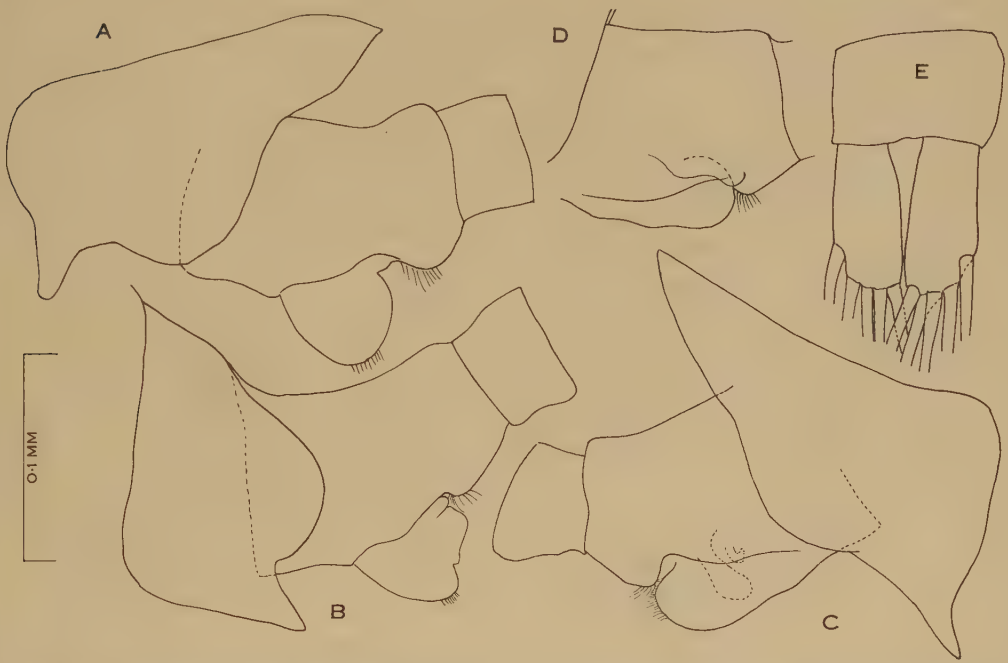


Fig. 10.—*Calamoecia salina* (Nicholls), ♀. *A–D*, lateral views of fifth thoracic and genital segments, showing various positions assumed by the ventral bulge; *E*, dorsal aspect of last urosome segment and furcal rami.

The outline of the right endopodite, considered as a whole, agrees well with Searle's drawing. However, he shows the endopodite to be 1-segmented, this condition also being indicated in the text (Searle 1911, p. 178), whereas in all specimens examined, including topotypes, it is boldly 2-segmented. The proximal segment is shorter than the distal one which bears a very conspicuous and highly characteristic protuberance on its outer edge, and terminates in 2 or 3 spines.

*Variation*

The Western Australian material differed from the remainder in the following minor points (Fig. 5*D*):

(1) On the middle segment of the exopodite of the male fifth right foot, the shorter of the two adjacent spines is considerably longer.

(2) The terminal spines on the endopodite of the same foot were longer.

*Occurrence*

(1) *Previous.*—VICTORIA: Yan Yean Reservoir and Essendon, Melbourne (Searle 1911).

(2) *Present.*—VICTORIA: Yan Yean and Toorourrong Reservoirs, Melbourne; Taylor's Lake, Horsham. SOUTH AUSTRALIA: The following reservoirs in the vicinity of Adelaide: Hope Valley, Happy Valley, Thorndon Park, Millbrook, Barossa Valley, Hindmarsh Valley. WESTERN AUSTRALIA: Farm dams; York.

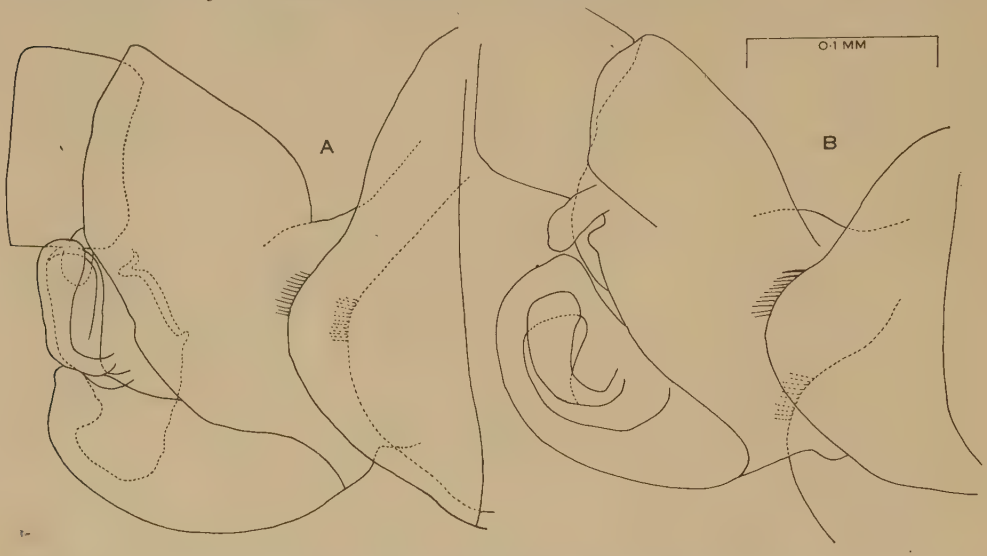


Fig. 11.—*Calamoecia attenuata* (Fairbridge), ♀. *A–B*, fifth thoracic and genital segments viewed laterally, *A* showing the internal bulbs extruded from the bulge.

CALAMOECIA SALINA (Nicholls)

Figs. 2*A–F*, 4*G*, 10*A–E*

*Brunella salina* Nicholls, 1944, pp. 6–8.

Type: Salt Lake, Beachport, S.A.; South Australian Museum.

*Description*

This species has been fully described by Nicholls (1944) and redescription is unnecessary. The author has examined the type material, and in addition, five female and three male specimens from the unmounted material from which the syntypes had originated. From this material, the above figures have been prepared.

The following points noted during examination of the above material supplement or verify Nicholls's account: Although the distal exopodite segment of the female fifth legs usually bears 2 unequal spines a specimen was observed with 3 unequal spines—there being an additional inner spine. The endopodite of this leg is slightly constricted along each edge in two places but is 1-segmented. In several cases the left endopodite of the male fifth feet appeared to be distinctly 3-segmented whereas in Nicholls's figures middle and distal portions are separated by a dotted line—presumably indicating indistinct segmentation.

*Remarks*

This is the most distinctive species of the genus, not only structurally, but, as is mentioned later, also ecologically. Both sexes can be recognized by the fact that, when non-geniculate antennules are extended backwards, the distal extremity does not reach beyond the posterior border of the first urosome segment. Additional distinctive features in the female are the number and nature of the spines on the terminal exopodite segment of the fifth legs, and the shape of the fifth thoracic segment. The male is the only one in the genus that can be recognized, at a glance, by the structure of the exopodite of the right fifth leg (see Fig. 2*F*).

It is noteworthy that the females of this species, unlike most, if not all, of the remaining species, have no suggestion of an attachment process for an egg-sac on the ventral aspect of the genital segment posterior to the bulge. This is further evidence that Nicholls's (1944) suggestion that the eggs are liberated directly into the water is almost certainly correct.

*Occurrence*

SOUTH AUSTRALIA: Salt Lake, Beachport.

## CALAMOECIA ATTENUATA (Fairbridge)

Figs. 3*A–D*, 11*A–B*

*Brunella attenuata* Fairbridge, 1945*b*, pp. 67–8.

Proposed neotype: ♂, Aust. Mus. Reg. No. P13488. Hypotypes: ♂, 2♀♀, Aust. Mus. Reg. No. P13489.

*Description*

This species has been fully described by Fairbridge (1945*b*), and little redescription is necessary. The author has examined 10 specimens of each sex collected on September 9, 1960, from Canningvale, Perth, this being very close to two of the type localities. The above figures have been drawn from this material.

The following points supplement or verify Fairbridge's account:

*Size.*—*C. attenuata* is probably the largest species of the genus so far described. Its males, unlike those of most of the remaining species, regularly exceed 1·0 mm in length. The average lengths for the specimens examined were 1·72 mm (females) and 1·48 mm (males). However, bearing in mind the cyclic length changes undergone by many freshwater calanoids, with a summer minimum and a winter maximum, these lengths would be close to maximal.

*Female.*—The fifth thoracic segment has rounded posterior extremities, and the genital bulge is large and smoothly rounded. The fifth thoracic segment of all specimens examined had the patches of posterior spines described by Fairbridge, but the dorsal patches were not always present, and spine patches other than these two were sometimes present. Because of this variation (and the fact that a spinulated fifth thoracic segment occurs as a variation in *C. tasmanica tasmanica*) this feature has not been exploited in the key to the females.

Fairbridge (1945*b*, pl. i, fig. 7) shows the terminal exopodite segment of the fifth leg as having 6 spines, the 4 inner ones of which are much shorter than a long terminal spine. Although this is not obviously the case, it is presumed that these spines have been deliberately truncated for ease of drawing. All the material examined had 5 subequally long spines to the inside of the short outermost one, as shown in Figure 3*A*. This is a feature of considerable taxonomic importance.

*Male.*—The fifth legs of specimens examined agree well with Fairbridge's description and figures, except that the extremity of the left exopodite is somewhat more complex in structure than he indicates. The distal inner corner is not turned over as a simple flap. The serrated lamella on the distal outer corner consists of 2 portions. The straight serrated portion figured by Fairbridge is continuous with a rounded portion with serrated edges, immediately adjacent to which the single spine takes its origin (see Fig. 3*D*).

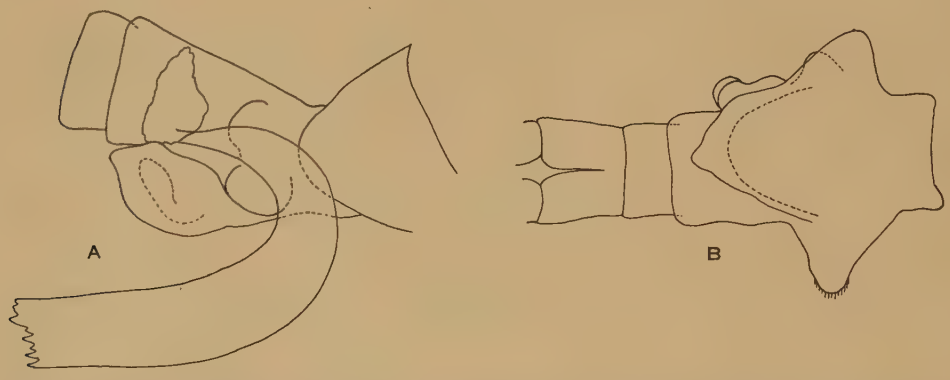


Fig. 12.—*Calamoecia gibbosa* (Brehm), ♀. *A*, fifth thoracic and genital segments viewed laterally, the proximal portion of a spermatophore being also shown; *B*, ventral aspect of urosome, showing the lateral outgrowths of the genital segment.

*Occurrence*

(1) *Previous.*—WESTERN AUSTRALIA: University, Perth; Swamp near Albany.

(2) *Present.*—WESTERN AUSTRALIA: Canningvale, Perth.

### CALAMOECIA GIBBOSA (Brehm)

Figs. 5*E–K*, 12*A–B*

*Brunella gibbosa* Brehm, 1950, pp. 252–3; 1953*a*, pp. 41–3.

Topotypes will be deposited in the Australian Museum.

This species was described in the first instance without figures (Brehm 1950) and subsequently with figures (Brehm 1953*a*). The author has examined 10 specimens of each sex collected on November 19, 1960, from Lake Dulverton, Tasmania, the type locality. The figures have been drawn from this material.

It would seem desirable to enlarge somewhat on Brehm's descriptions, which were rather brief, and to make one or two corrections.

*Description of Male*

*Fifth legs.*—The endopodite of the right leg was described and figured by Brehm as being 2-segmented. However, in all specimens examined it was clearly 3-segmented, although the proximal segment, being the smallest, is sometimes obscured by the proximal segment of the exopodite. The right endopodite usually terminates in 4 setae. The proximal segment of the right exopodite is relatively short, being only half the length of the middle segment, and bears a stout outer spine. On the middle segment, there arises from the posterior distal aspect a prominent spine. The distal segment is a claw bent almost through a right angle and bearing a prominent secondary spine near the base.

The left exopodite is 2-segmented, the distal segment being the shorter of the two, having a rounded extremity bearing minute denticles and a twisted construction. Proximal to the denticulated region are inserted 2 spines of unequal length. The left endopodite is 1-segmented, exceeds the exopodite in length and usually terminates in 4 setae.

*Description of Female*

*Fifth thoracic and genital segments.*—The fifth thoracic segment has rounded posterior extremities which do not extend very far posteriorly along the side of the genital segment. The latter is remarkable for its very prominent lateral outgrowths. There is a single one of the left side bearing minute hairs at its extremity. On the right side there are 2 outgrowths, one above the other, of which the ventral one is the larger. The genital operculum is well developed viewed laterally and is asymmetrical viewed ventrally, there being a bulge on the right side.

*Fifth legs.*—The inner process of the middle exopodite segment is very strongly developed and markedly recurved. In some cases this process is even more strongly developed (cf. Fig. 5*J* with Fig. 5*K*). The distal exopodite segment bears only 2 spines—a short outer one, and a much longer terminal one which is bent inward. The endopodite is usually 2-segmented but the segmentation may be indistinct or lacking, the 1-segmented condition also being observed. The number of endopodite setae is variable, the maximum number being 8—usually 2 on the proximal segment and 6 on the distal one.

*Occurrence* (previous and present)

TASMANIA: Lake Dulverton.

### CALAMOECIA TRIFIDA, sp. nov.

Figs. 1*F–H*, 4*K*, 13*A–F*

Holotype ♂, Aust. Mus. Reg. No. P13490; allotype ♀, Aust. Mus. Reg. No. P13491; paratypes 12♂♂, 12♀♀, Aust. Mus. Reg. No. P13492. All types from Somerset Dam, August 16, 1959.

*Description of Female*

*Size.*—Length, inclusive of furcal setae, 1·29 mm (average of 12 measurements).

*Cephalothorax.*—Head with distinct nuchal groove, and distinct from the 5 thoracic segments the last of which has rounded posterior extremities. General form

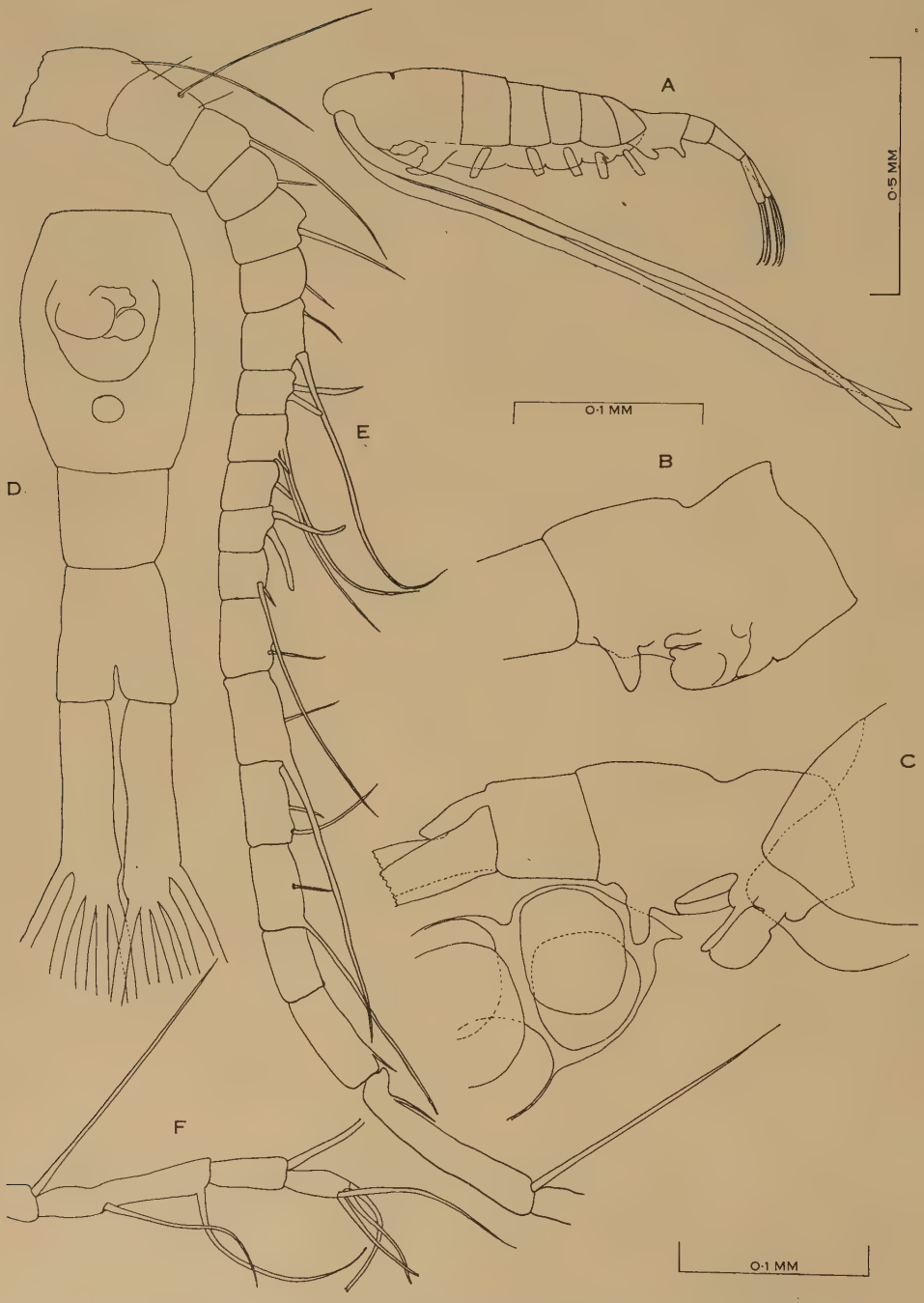


Fig. 13.—*Calamoecia trifida*, sp. nov. *A*, ventrolateral aspect of whole ♀; *B*, lateral view of genital segment of ♀ with ventral bulge closed; *C*, fifth thoracic segment and urosome of ♀, showing bulge open and attachment of egg sac to pillar on genital segment; *D*, ventral aspect of ♀ urosome; *E*, dorsal aspect of ♂ geniculate antennule; *F*, distal segments of geniculate antennule.

and proportion of these as in Figure 13*A*. Antennules long, extending beyond the posterior extremity of the furcal setae.

*Abdomen.*—Ventral swelling on genital segment flattened beneath, being less rounded or bulbous and less pronounced than in most species (cf. Fig. 6*D*). This protuberance apparently dehisces from the bulk of the segment along its initial posterior attachment to hang obliquely downwards from the persisting anterior attachment. On the posterior ventral aspect of the genital segment behind the bulge is a stout bluntly pointed projection at right angles to the long axis of the segment. This serves to give attachment to the egg sac. At the time of collection the latter contained an average number of 9 eggs (12 determinations).

*Fifth legs* (10 examined).—Exopodites typical of family in segmentation and large inner spine of middle segment, proximal segment bears a single outer spine which the middle segment usually lacks. The distal exopodite segment bears invariably (in 20 examined) 4 spines—a short outer one, a long terminal one, and 2 subequal inner ones approximately half the length of the longest. Endopodite distinctly 2-segmented, proximal segment with usually 2 inner setae, distal segment with usually 6 setae.

*Description of Male*

*Size.*—Length, as above, 0·91 mm (average of 11).

*Cephalothorax.*—Head and thorax proportions as in female. Details of the armature of the geniculate antennule are shown in Figure 13*E–F*.

*Fifth legs.*—The right exopodite is typical of the genus in its segmentation and termination in a long claw. Halfway along the concave side of the latter is located a raised knob just proximal to which is a short incurved spine. Proximal segment is constricted proximal to its expanded distal extremity and bears a single outer spine. In these details the species closely resembles *C. tasmanica*. Middle segment bears a knob at its inner proximal edge and an outer distal spine. The right endopodite is 3-segmented and terminates in 3 short spines. The distal protopodite segment bears a blunt inner projection.

The left leg is quite unlike that in any of the other species, and is essentially trifid in appearance. There is a long, slightly curved, inner process from the distal segment of the protopodite, smooth on the convex surface, 2–3-lobed on the concave side. This extends to a point almost level with the distal extremity of the solid portion of the exopodite. The latter is 2-segmented with the distal segment much shorter than the proximal, and is produced distally into a thin, transparent, shovel-like process finely serrated around the edges. Between the exopodite and protopodite process lies a club-like endopodite, broader distally than proximally, and somewhat constricted and bent (but apparently not segmented) near the middle. This reaches almost to the end of the exopodite process and terminates in 3 short spines.

*Remarks*

The closest relative of this species appears to be *C. tasmanica* from which, however, it is readily distinguished in the male fifth legs by the relatively much

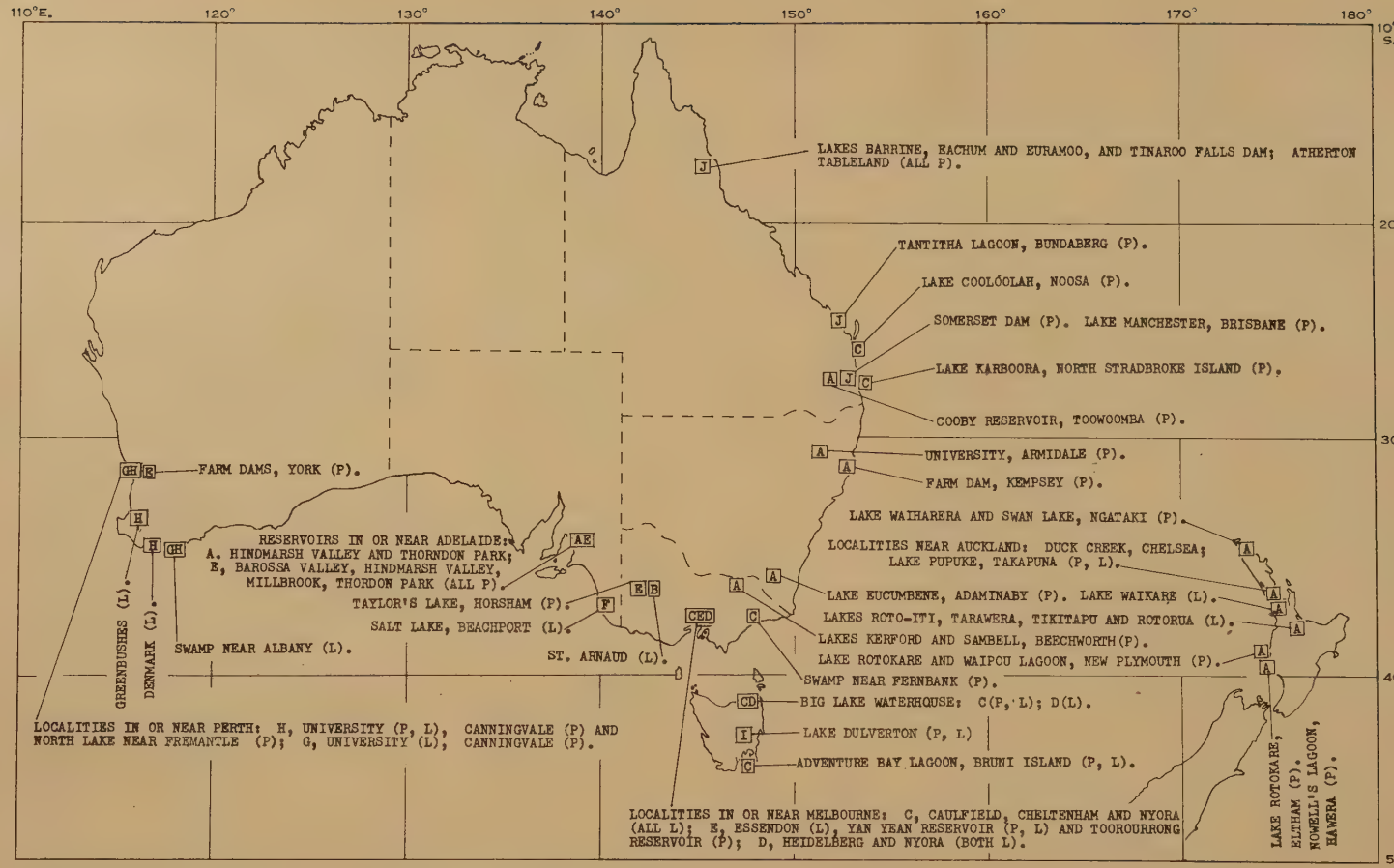
110°E.
120°
130°
140°
150°
160°
170°
180°
10° S.
20°
30°
40°
50°
LAKES BARRINE, EACHUM AND EURAMOO, AND TINAROO FALLS DAM; ATHERTON TABLELAND (ALL P).
TANTITHA LAGOON, BUNDABERG (P).
LAKE COOLÓOLAH, NOOSA (P).
SOMERSET DAM (P). LAKE MANCHESTER, BRISBANE (P).
LAKE KARBOORA, NORTH STRADBROKE ISLAND (P).
COOBY RESERVOIR, TOOWOOMBA (P).
UNIVERSITY, ARMIDALE (P).
FARM DAM, KEMPSEY (P).
FARM DAMS, YORK (P).
LAKE WAIHARERA AND SWAN LAKE, NGATAKI (P).
LOCALITIES NEAR AUCKLAND: DUCK CREEK, CHELSEA; LAKE PUPUKE, TAKAPUNA (P, L).
RESERVOIRS IN OR NEAR ADELAIDE: A. HINDMARSH VALLEY AND THORNDON PARK; E, BAROSSA VALLEY, HINDMARSH VALLEY, MILLBROOK, THORDON PARK (ALL P).
LAKE EUCUMBENE, ADAMINABY (P). LAKE WAIKARE (L).
TAYLOR'S LAKE, HORSHAM (P).
LAKES ROTO-ITI, TARAWERA, TIKITAPU AND ROTORUA (L).
SALT LAKE, BEACHPORT (L).
LAKES KERFORD AND SAMBELL, BEECHWORTH (P).
LAKE ROTOKARE AND WAIPOU LAGOON, NEW PLYMOUTH (P).
GREENBUSHES (L).
DENMARK (L).
SWAMP NEAR ALBANY (L).
ST. ARNAUD (L).
SWAMP NEAR FERNBANK (P).
BIG LAKE WATERHOUSE: C(P, L); D(L).
LAKE DULVERTON (P, L)
ADVENTURE BAY LAGOON, BRUNI ISLAND (P, L).
LOCALITIES IN OR NEAR PERTH: H, UNIVERSITY (P, L), CANNINGVALE (P) AND NORTH LAKE NEAR FREMANTLE (P); G, UNIVERSITY (L), CANNINGVALE (P).
LOCALITIES IN OR NEAR MELBOURNE: C, CAULFIELD, CHELTENHAM AND NYORA (ALL L); E, ESSENDON (L), YAN YEAN RESERVOIR (P, L) AND TOOROURRONG RESERVOIR (P); D, HEIDELBERG AND NYORA (BOTH L).
LAKE ROTOKARE, ELTHAM (P). NOWELL'S LAGOON, HAWERA (P).

Fig. 14.—Localities and distribution of the Species. (*P*), localities recorded during the present survey. (*L*), localities recorded in previous literature. *A*, *C. lucasi*; *B*, *C. australica*; *C*, *C. tasmanica tasmanica*; *D*, *C. australis*; *E*, *C. ampulla*; *F*, *C. salina*; *G*, *C. attenuata*; *H*, *C. tasmanica subattenuata*; *I*, *C. gibbosa*; *J*, *C. trifida*.

longer process from the left protopodite, the terminal process on the left exopodite, and the reduction in the number and length of the terminal spines of the left and right endopodite.

*Occurrence*

QUEENSLAND: Lake Manchester, Brisbane; Somerset Dam; Tantitha Lagoon, Bundaberg; the following localities on the Atherton Tablelands: Lakes Eacham, Barrine, and Euramoo, and Tinaroo Falls Dam.

## IV. Distribution of the Species, Zoogeography, and Ecology

(see Fig. 14)

It is surprising that the type species, *C. lucasi*, although apparently widely distributed in Australia, has not hitherto been recorded from this country. Its presence here provides a further zoogeographic bond between the fresh water faunas of Australia and New Zealand. Thus *Boeckella* and *Calamoecia*, the two chief calanoid genera of the inland waters of New Zealand and the southern half of Australia, each have one species common to both countries, namely *B. triarticulata* Thomson and *C. lucasi* respectively. *C. lucasi* shows a much wider north–south distribution than previously indicated, extending from Hawera (lat. 40° S.) to Toowoomba (lat. 28° S.). It should be pointed out, however, that the two northernmost records for this species were from high altitude localities, namely, Toowoomba (2000 ft) and Armidale (3500 ft) where temperatures are lower than low-lying regions of similar latitude. It is probable that this factor permits the species to extend as far northwards as this. There is evidence that *C. lucasi* replaces other species of *Calamoecia* with a seasonal fall in water temperatures. Thus collections from Thorndon Park Reservoir, Adelaide, made on May 5, 1960, contained *C. ampulla* but collections from the same locality made on June 14, 1960, contained *C. lucasi*.

*C. tasmanica* has an even wider north–south distribution extending from Adventure Bay, Bruny Island (lat. 43° S.) to Lake Cooloolah, Queensland (26° S.). This species thus tolerates a wide range (probably in excess of 20°C) of water temperatures. It was collected on June 12, 1960, from a lagoon on Bruny Island the temperature of which was 9°C (A. Phillips, personal communication) and from Lake Cooloolah on April 30, 1960, when the temperature was 25°C. This lake would have a midsummer temperature of approximately 30°C. The important factor in the distribution of *C. tasmanica* appears to be fairly close proximity to the sea and presumably a salinity slightly higher than the normal range for freshwater. Its typical habitat is a peaty lagoon set back only a relatively short distance from the sea, although Brehm (1953*b*) records *C. tasmanica subattenuata* from as far inland as 40 miles.

*C. trifida* extends in distribution from Lake Manchester (27° S.) to Tinaroo Falls Dam (17° S.), but, as in the case of *C. lucasi*, the northernmost records are from high-altitude localities—in this case from above 2000 ft on the Atherton Tablelands. The temperature of the waters from which *C. trifida* is recorded does not normally fall below approximately 14–15°C in midwinter. The remaining species appear to have a more limited north–south distribution than the three mentioned

above. However, large areas of Australia have not been sampled, and for none of the species is the full distribution pattern known. Thus, how far north the genus extends in Northern Territory and Western Australia is unknown. With regard to east–west distribution, it appears that *C. attenuata* and *C. tasmanica subattenuata* are confined to Western Australia and that the majority of eastern species (not *C. ampulla*) are absent from that State.

Brehm (1953*a*) considered that the new species he described, which included *C. gibbosa*, would not be endemic to Tasmania. He stated: "They will certainly be found in adjacent parts of the Australian Continent". While the type of distribution envisaged by Brehm is undoubtedly true of *C. tasmanica* and *C. australis*, it seems quite possible that *C. gibbosa* is endemic to Tasmania. It is to be expected that the chances of mainland species occurring in Tasmania are greater at an altitude lower than that (1700 ft) from which *C. gibbosa* is recorded.

Fairbridge (1945*b*, p. 77) commented that the genus ". . . is confined within an area inside the geographical range of *Boeckella* . . ." and that it seemed ". . . to have spread freely along the lines of latitude but not in a North–South direction . . .". It is doubtful whether the former statement is still true, since although *Boeckella minuta* Sars occurs along with *C. trifida*, in Lake Manchester and Somerset Dam, no species of *Boeckella* accompanied *C. trifida* in collections from Bundaberg and the Atherton Tablelands. Thus the indications are that *C. trifida* extends outside the range of *Boeckella*. With regard to the second statement it would appear that studies of the genus, rather than the genus itself, spread more freely along the lines of latitude to which Fairbridge referred, than in a northerly direction. However, Fairbridge (1945*a*, p. 40) discussing the Australian distribution of *Boeckella*, did point out that little investigation had been made in the subtropical regions. *Calamoecia* extends to at least as far north as 25° S. at low altitudes for *C. trifida* occurs close to Bundaberg. At the same time, *Calamoecia* apparently does not extend in distribution to either the low-lying coastal regions or the more inland regions of the far north of Australia. Collections from Mt. Isa, Mary Kathleen, and Ayr, which lie approximately along the line of latitude 20° S., have failed to yield *Calamoecia*. These collections are dominated by essentially northern hemisphere faunal elements, so that *Boeckella* and *Calamoecia* are completely replaced by *Diaptomus lumholtzi* Sars in limnetic regions. The latter species was described by Sars from Gracemere Lagoon, near Rockhampton, which lies almost on the Tropic of Capricorn. Thus, considering low-lying regions only, and especially those that are relatively coastal, the northern limit of *Calamoecia* lies between 23° 30′ S. and 25° S. In the region bounded approximately by 24° S. and 29° S. (vicinity of Casino, N.S.W.) *Diaptomus orientalis* Brady overlaps with *Calamoecia* and *Boeckella*. However, this northern species does not appear to compete with species of the southern genera in the limnetic regions of lakes and dams, rather it appears limited to ponds and pools.

It is probable that Fairbridge's (1945*b*) comments concerning the relatively restricted north–south distribution of *Calamoecia* were influenced by Henry's (1922) complete failure to record *Calamoecia* when monographing the New South Wales freshwater copepods. This is puzzling, for the genus is certainly present there, and furthermore Henry was aware of its existence, having described a species of the

genus from elsewhere (Henry 1924). Two possible explanations are offered for this omission. Firstly, that in field collections *Calamoecia* was usually mixed with *Boeckella*, and that it was overlooked as the earlier copepodid stage of *Boeckella* because of its small size. Unless egg-bearing females are present this can happen, especially when *Calamoecia* comprises only a small portion of a catch. A second explanation to the above is that Henry relied too much on artificial hatching from dried mud—a method that may not be suitable for *Calamoecia*. In this respect it is noteworthy that although Sars described many Australian entomostracan species, including copepods, by artificial hatching from dried mud, he did not describe one species of *Calamoecia* raised in this manner. *Calamoecia* is predominantly limnetic in habit and it is possible that the difficulty of realizing true limnetic conditions in aquaria make them unsuitable for rearing the genus.

Although predominantly a freshwater genus, the tendency of *Calamoecia* to extend into salt water is noteworthy. It is better described as being inland or "non-marine", rather than freshwater. Consideration of the genus as being purely the latter probably led Jolly (1955) and Brehm (1959) to overlook *C. salina* which was found in a salt lake at Beachport, South Australia (Nicholls 1944). The tendency of *C. tasmanica* to inhabit slightly brackish water has been mentioned above. In showing this tendency, the genus probably overlaps in salinity range with *Gladioferens*, *Sulcanus*, and *Pseudodiaptomus*, which are euryhaline genera exhibiting a reversed tendency to spread into freshwaters from marine or brackish. There do not appear to be any Australasian records of *Boeckella* species from anything but fresh water.

Sewell (1948) states that the distribution of the species of *Calamoecia* (together with *Gladioferens* and "such marine species as *Labidocera cervi* Kramer"), "points to a transfer of species from the New Zealand region round the Tasman Sea and along the east coast of Australia, by the East Australian Current, and then westward along the south coast of Australia at some earlier period". However, it would seem improbable that ocean currents could play a major part in the dispersal over this distance, of a genus in which no truly marine species are known. The observed distribution of *Calamoecia* is certainly capable of explanation without invoking ocean currents. Thus it is quite possible that the sole New Zealand species, which also occurs on the south-east coast of Australia, was dispersed in the opposite direction to that suggested by Sewell—across the Tasman Sea in the direction of the prevailing westerly wind.

Riek (1959), dealing with the Australian freshwater crustacean fauna, makes reference among the calanoids to *Boeckella* and *Diaptomus* but not to *Calamoecia*. The latter genus, however, must be considered even more distinctive of the Australian freshwater fauna than *Boeckella*; it is entirely confined in distribution to the Australasian zoogeographical region, and, with the exception of a single species, is completely limited to Australia. In contrast to this, *Boeckella* exhibits in addition to its Australasian occurrence, a South American and Mongolian distribution (Fairbridge 1945*a*).

The number of species of *Calamoecia* is approximately half the number of Australasian species of *Boeckella*. The assessment of the relative ecological importance of these two genera cannot yet be made, but it is clear that both are important dominants in the limnetic region of lentic environments. In limnetic collections

from 12 localities in New Zealand within the region of overlap of the two genera, *Boeckella propinqua* occurred at four localities and *Calamoecia lucasi* at five (Bayly 1959). In these collections the two species were never taken together. On the other hand several Australian collections have shown *Calamoecia* and *Boeckella* to be coexisting in the plankton. The factors determining which will be present in a given situation, and when coexisting, what determines the relative proportions, have yet to be elucidated.

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## LIST OF SPECIES OF THE GENUS CALAMOECIA

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# THE AUSTRALIAN PORTUNIDS (CRUSTACEA: PORTUNIDAE)

## V. RECENT COLLECTIONS

By W. STEPHENSON*

[*Manuscript received January* 18, 1961]

*Summary*

Recent collections from Australian waters have contained four new species which are described and, in addition, seven species not recorded previously, five of which have merited full description. In addition the known ranges of several Australian species have been extended, including 14 new records for Western Australia. Minor comments on structure and coloration of certain species are also given.

## I. INTRODUCTION

The four previous papers in this series (Stephenson and Hudson 1957; Stephenson, Hudson, and Campbell 1957; Stephenson and Campbell 1959; and Stephenson and Campbell 1960) dealt with collections in Australian institutions up to January 1956, supplemented by recent collections made by or held at the University of Queensland. Since 1956 interesting specimens have been obtained from eastern and western Australian waters (especially the latter) and these are reported upon in the present paper.

Descriptions of first pleopods of males and the terminology applied to different areas of the carapace follow the earlier papers. The order of presentation of families and genera follows Stephenson and Campbell (1960).

When species were adequately described in the previous papers of this series the synonymy is greatly abbreviated and data on distribution are stressed. In other cases descriptive material is given, particularly for new species and those now recorded for the first time from Australia.

## II. RECORDS AND DESCRIPTIONS OF SPECIES

### Subfamily **CARCININAE** Alcock

### Genus NECTOCARCINUS A. Milne Edwards

#### NECTOCARCINUS SPINIFRONS, sp. nov.

Figs. 1*A*, 2*G*; Plate 1, Fig. 1; Plate 4*A*

*Material Examined*

WESTERN AUSTRALIA: ♂ holotype (13 mm), 4 miles W. of Cape St. Cricq, Dorre I. Shark Bay, R. W. George, 16.v.1960, dredged 40 fm (W. Aust. Mus. Reg. No. 47–60); ♀ allotype (21 mm) data as above (W. Aust. Mus. Reg. No. 47(*c*)–60); ♀ (ovigerous) (18 mm), ♀ (20 mm) data as above (W. Aust. Mus. Reg. No. 47(*b*)–60).

*Material illustrated.*—Abdomen and pleopod (holotype), dorsal view (allotype).

* Department of Zoology, University of Queensland, Brisbane.

*Description*

*Front.*—Two broad protruding lobes, separated by a deep median notch, and each distinctly separated from the relatively small inner supraorbital lobes. Each frontal lobe is set slightly obliquely and has an almost concave anterior border beset with short, sharp spinules and bearing a thin line of elongate hairs.

*Anterolateral teeth.*—Four, all sharp, the first the stoutest, the fourth the smallest, the third the most protruding.

*Carapace.*—Long, breadth 1·15–1·2 times length. Uniformly and somewhat sparsely covered with short, stout hairs underlying a general granulation and with the regions very clearly marked. No transverse ridges are present and there is only a slight degree of concentration of granules in the protogastric regions.

*Basal antennal joint.*—Narrow, with a granular base and completely excluding the flagellum from the orbit. This joint is not completely fused with the orbit and can be moved independently with greater ease than in *N. tuberculosus*.

*Chelipeds.*—Unequal, with the right slightly larger than the left. Arm short and curved, bearing 4 or 5 spines (excluding spinules) on its posterior border, with the distal one inflated. The anterior border bears a single spine near the tip. Wrist very broad and bearing on its inner side a large spine with secondary spinules on its distal surface. Numerous small spines, spinules, or spiniform granules are present on the upper surface. The different surfaces of the hands are not clearly demarcated excepting for an upper inner boundary separating inner and outer surfaces. Near its distal end this boundary bears a single conspicuous spine or enlarged tubercle. The outer surface of the hand bears irregular rows of spiniform granules but no carinae. Similar but smaller granules are present on the under and inner surface of the hand. Fingers short, stout, and strongly carinated.

*Walking legs.*—Elongate, flattened, and each with a long thin dactylus (length 7–9 times breadth).

*Fifth leg.*—Flattened, with dactylus lanceolate and propodus ovate. Both segments are fringed with elongate hairs.

*First male pleopod* (based on a single specimen).—Moderately stout without marked lateral curvature and twisted in a corkscrew fashion. A band of spinules begins on the inner surface about half the way up the appendage, then passing to the lower surface to reappear at and just below the tip.

Apart from being thinner in its proximal half, the appendage greatly resembles that of *N. tuberculosus*.

*Colour.*—After 3 months in alcohol, the general colour is pale brown, with rose suffusions as follows: eye-stalks, tips of first two anterolateral teeth, anterior portions of the two epibranchial and the median cardiac prominences, certain spiniform granules on the upper surface of hand, bands on most segments of walking legs. Fingers of chelipeds sooty brown in their distal halves.

Fig. 1.—Left first male pleopods; low power views of entire appendages. *A, Nectocarcinus spinifrons; B, Parathranites orientalis; C, Lissocarcinus laevis; D, L. orbicularis; E, Lupocyclus tugelae; F, Portunus argentatus; G, P. curvipenis.*

*Comments*

This species keys out as *N. tuberculosus* (A. Milne Edwards) (see Stephenson and Campbell 1960, p. 83) but differs obviously in the form of the front, and in possessing a conspicuous spine or tubercle on the upper inner border of the hand of the cheliped.

It differs from the other species of the genus in the relative mobility of the basal antennal joint which could not accurately be described as "fused to the front". Also it is somewhat atypical in that the fifth leg shows slightly increased adaptations for swimming. However, its resemblances to the other species are too close to justify the erection of a new genus. This applies to the form of the male pleopods and to the curiously inflated terminal spine on the distal end of the posterior margin of the arm.

## Subfamily **MACROPIPINAE** Stephenson & Campbell

### Genus OVALIPES Rathbun

#### Ovalipes molleri (Ward)

*Aeneacancer molleri* Ward, 1933, pp. 381–3, pl. xxiii, fig. 11. McNeill, 1953, p. 93, pl. 7, figs. 1, 2.

*Ovalipes molleri* Stephenson and Campbell, 1960, pp. 88–91, figs. 1*D*, 2*F*; pl. 2, fig. 3; pl. 5*F*.

*Material Examined*

NEW SOUTH WALES: 6♂♂ (23–30 mm) otter trawled mud bottom 125 fm, off Port Stephens, Dr. A. A. Racek, 3.vii.1959 (Aus. Must. specimens).

*Comments*

This is only the third collection of this species, and contains the first known specimens less than 50 mm in breadth. They differ from larger specimens as follows:

(1) Less iridescent, although iridescence still plainly visible.

(2) Thin areas of carapace detectable but semitransparent, rather than transparent.

(3) Orbital region broader. The distance between the two first anterolateral teeth is about two-thirds of the carapace breadth, as against a little less than half in the previous specimens.

(4) Carapace relatively narrower. In the present specimens the breadth is 1·17 times the length (1·15–1·19) as against *c.* 1·25 in previous specimens.

In all other features including those of the male abdomen and pleopods the specimens clearly belong to *O. molleri*.

It should be noted that item (2) above modifies the specific description and diagnostic features. The carapace proportions of the smaller specimens bring this species even closer to *O. iridescens* (Miers 1886—see his pl. xvii, fig. 2) although it is still clearly distinct.

A total of 34 male specimens as against a single female have now been collected, all off south-east Australia, and all in fairly deep water.

Fig. 2.—Left first male pleopods; *A–F* low power views of entire appendages, *G–I* high power views of tips, the upper surfaces to the left of the scale line and under surfaces to the right. *A*, *Portunus pseudoargentatus*; *B*, *P. rugosus*; *C*, *P. tenuicaudatus*; *D*, *Thalamita dakini*; *E*, *T. granosimana*; *F*, *T. parvidens*; *G*, *Nectocarcinus spinifrons*; *H*, *Parathranites orientalis*, upper surface; *I*, *Lissocarcinus laevis*, under surface.

## Genus PARATHRANITES Miers

*Parathranites* Miers, 1886, pp. 186–7 (as subgenus of *Lupocyclus* Adams & White, 1849). Alcock, 1899, pp. 16–17. Stephenson and Campbell, 1960, p. 88 (in key).

The genus is adequately defined by Alcock (1899) excepting that it should be modified to include *P. hexagonum* Rathbun which possesses six anterolateral teeth. Diagnostic features were given in Stephenson and Campbell (1960). No specimens of this genus have hitherto been recorded from Australian waters.

### Key to Indo-west-Pacific Species of Genus Parathranites

1. Merus of natatory legs very little longer than broad; penultimate segment of male abdomen much longer than broad .....
.....*P. latibrachium* Rathbun (1906, p. 868, fig. 26*a,b*) (not recorded from Australia)

Merus of natatory legs much longer than broad; penultimate segment of male abdomen broader than long .....2

2(1). 6 anterolateral teeth; carapace relatively broad. ($l/b$ = 55%, including last tooth) ....
*P. hexagonum* Rathbun (1906, pp. 867–8, fig. 25, pl. xii, fig. 3) (not recorded from Australia)

5 anterolateral teeth, carapace relatively narrow ($l/b$ = 70%, including last tooth) .....
..... *P. orientalis* Miers (1886)

### Parathranites orientalis Miers

Figs. 1*B*, 2*H*; Plate 1, Fig. 2; Plate 4*B*

*Lupocyclus* (*Parathranites*) *orientalis* Miers, 1886, pp. 186–7, pl. xvii, fig. 1, 1*a,b,c*.
*Parathranites orientalis* Miers. Alcock, 1899, pp. 17–18. Rathbun, 1911, p. 204 (record only). Yokoya, 1933, p. 178 (record only). Sakai, 1936, p. 119, pl. 32, fig. 2; 1939, pp. 376–7, pl. xliii, fig. 2. Barnard, 1950, pp. 148, 149, fig. 29*i–l*.

*Material Examined*

NEW SOUTH WALES: 2♂♂ (24, 25 mm) otter trawled mud, 125 fm off Port Stephens, Dr. A. A. Racek, 3.vii.1959 (Aust. Mus. specimens). *Ovalipes molleri* was present in the same collection.

*Material illustrated.*—Larger specimen.

*Description*

*General.*—Considered unnecessary.

*Male pleopod* (based on two specimens).—Smoothly curving and regularly tapering to a pointed tip. Beyond the basal lobes on the outer surface about one-fifth the distance up the appendage there is a row of about 25 long bipinnate hairs. About one-third of the way up, there are a few (2) short bristles followed by an elongate row of distantly spaced short recurved spinules. In profile view these become decreasingly common and decreasingly conspicuous as one proceeds to the tip; actually the row moves from the outer to the under surface of the appendage. This under surface bears an irregular triple row of short recurved spinules over the distal half of the appendage, these continuing practically to the tip. On the inner surface just beyond the basal lobes there are a few bipinnate hairs which are much shorter than those on the outer side. Apart from these the inner surface is bare.

The terminal armature consists of a few recurved spinules on the upper surface and 4 or 5 showing through from the under surface.

*Comments*

As compared with Miers (1886) the only differences noted are: (1) present specimens have slightly longer and more pointed ultimate segment of male abdomen; (2) inner angles of the suborbital margin which are described as "dentiform" by Alcock (1899, p. 17) are not shown in Miers (1886, pl. xvii, figs. 1, 1*a*, where they should be visible in dorsal view).

As compared with Alcock (1899) the only differences noted were: (1) there is a spine instead of a spinule firstly on the posterior border of the arm near its distal end, and secondly on the outer surface of the wrist, and (2) the penultimate segment of the male abdomen is distinctly broader than long.

There are no differences compared with Sakai's (1939) diagnosis, but several as compared with his plate (pl. xliii, fig. 2). These are: (1) Sakai figures the frontal teeth as relatively broad and triangular; (2) the upper orbital border is differently shaped; (3) the last anterolateral teeth are less differentiated from the remainder; (4) the spine at the junction of the posterior and posterolateral borders of the carapace is less conspicuous, and (5) no spine is visible on the anterior border of the arm in the dorsal view of the entire animal. This last feature is mentioned in Sakai's text, and one can only conclude that his plate is inaccurate in this respect and possibly in the others.

*Distribution*

This is the first Australian record. The species was known previously from the Ki Islands and Admiralty Islands (Miers 1886), Indian waters and the Andamans (Alcock 1899), Solomon Bank (Rathbun 1911), Japanese waters (Yokoya 1933; Sakai 1936, 1939). All records are from reasonably deep waters.

## Subfamily **CAPHYRINAE** Alcock

### Genus CAPHYRA Guérin

### Caphyra yookadai Sakai

Plate 1, Fig. 3

*Caphyra yookadai* Sakai, 1933, pp. 141–3, pl. xiii, fig. 3; 1939, p. 378, pl. xliii, fig. 4. Stephenson and Campbell, 1960, pp. 102–4, figs. 1*I*, 2*K*, 3*H*; pl. 4, fig. 1; pl. 5*K*.

*Material Examined*

QUEENSLAND: ♂ 7 mm; from tentacles of brown alcyonarian (? *Microspicularia*) below L.W.S., Myora, Moreton Bay, December 1959, Miss J. H. Bryan (Zoology Department, University of Queensland, specimen presented to Queensland Museum).

*Comments*

The locality and habitat are identical with the only two Australian specimens known, which were collected by Mr. J. S. Hynd in 1946.

The colour alive is described by the collector as "shiny white with pottery blue blotches", and this contrasts with Sakai (1939, pl. xviii, fig. 4) who recorded a whitish pink base with brown mottling.

Sakai figured a dense row of setae on the propodus of the fourth leg. On the present specimen as in the previous two, only a few short scattered setae are present in the appropriate area and there are no indications of loss by damage.

The previous description (Stephenson and Campbell 1960) was misleading as regards carinae on the wrist. There are the two usual carinae on the upper surface, and in addition two conspicuous ones on the outer surface, as Sakai (1939, fig. 2) has figured. The moveable finger also bears a sharp, almost lamelliform carina.

The Moreton Bay specimens are so close to Sakai's *Caphyra yookadai* to justify retention in that species although the colour differences are greater than expected.

## Genus LISSOCARCINUS Adams & White

### Lissocarcinus laevis Miers

Figs. 1*C*, 2*I*; Plate 1, Fig. 4; Plate 4*C*

*Lissocarcinus laevis* Miers, 1886, pp. 205–6, pl. xvii, figs. 3, 3*a*, 3*b*. Henderson, 1893, p. 378. Alcock, 1899, p. 21. Rathbun, 1906, p. 869, fig. 27. Laurie, 1906, p. 411. Urita, 1926, p. 9. Sakai, 1934, p. 302, fig. 16; 1936, p. 121, fig. 57. Leene, 1938, p. 9. Sakai, 1939, pp. 380–1, pl. xlv, fig. 2. Edmondson, 1951, p. 220; 1954, p. 230–1, fig. 7*d–f*.

*Material Examined.*

WESTERN AUSTRALIA: ♂ (7 mm) Maud Landing, NW. coast, R. D. Royce, 20.v.1960, dredged 10 fm on weed, sand, rock (W. Aust. Mus. Reg. No. 109(*b*)–60).

*Description*

This species has been adequately described (e.g. Sakai 1939) and is clearly recognizable when fresh by its characteristic colour pattern. It is also distinguished from the two other species recorded previously from Australia, *L. polybioides* Adams & White and *L. orbicularis* Dana, by (1) the form of the front which is divided into two truncate lobes (in *L. polybioides* and *L. orbicularis* the front is medially produced) and (2) the upper surface of the palm of the cheliped not bearing carinae (as against bearing two carinae).

*First male pleopod* (based on a single specimen).—Short, extremely stout, with the narrowest portion near the centre and with a slightly flared tip. Beyond the basal lobes on the outer side, completely bare up to and including the tip, i.e. with no terminal armature visible in profile view. Inner surface with scattered hairs followed by the terminal armature which consists of an extremely well-developed fringe of elongate forwardly directed spinous bristles. These are longest and also most curved opposite the flaring of the tip and continue on to and round the edge of the tip. Approximately 35 are visible in profile view. The upper surface of the appendage is bare but on the under surface spinous bristles are present, being densely

Fig. 3.—Tips of left first male pleopods. The upper surfaces to the left of the scale lines and the under surfaces to the right. *A*, *Lissocarcinus orbicularis*; *B*, *Lupocyclus rotundatus*; *C*, *L. tugelae*; *D*, *Portunus argentatus*; *E*, *P. curvipenis* (right pleopod reversed); *F*, *P. pseudoargentatus*; *G*, *P. rugosus*; *H*, *P. tenuicaudatus*; *I*, *Thalamita dakini* (upper surface only).

distributed over the entire surface near the tip, but becoming increasingly restricted to the inner surface and also becoming smaller as one proceeds proximally.

Edmondson (1954, fig. 7*e,f*) has figured the male pleopod in this species recognizably but somewhat inaccurately.

*Distribution*

This species has not been recorded previously from Australia but extends from Ceylon (Laurie 1906) to Japan (Sakai 1939) and Hawaii (Edmondson 1954).

## Lissocarcinus orbicularis Dana

Figs. 1*D*, 3*A*

*Lissocarcinus orbicularis* Dana 1852*a*, p. 86; 1852*b*, p. 288, pl. xviii, figs. *a–e*. Edmondson, 1954, p. 230, figs. 6*b*, 7*a–c* (fig. 7*b–c* male pleopod). Stephenson and Campbell, 1960, p. 95, pl. 3, fig. 2 (synonymy).

*Material Examined*

QUEENSLAND: 2 ♂♂ (9, 10 mm) Heron I., J. Bishop, 10,11.viii.1960 in association with large, brown, warty holothurian.

*Material illustrated.*—Pleopod of larger male.

*Description*

The above specimens are the first males recently obtained from Australia and since Edmondson (1954) while figuring the male pleopods does not describe them, a description and figures are considered necessary.

*First male pleopod* (based on two specimens).—Base robust; shaft curved and slightly tapering, and bearing a relatively short subterminal membrane on the inner surface. Beyond the basal lobes bare to the tip apart from a few microscopic spinules. Subterminally on the under surface there are minute spinules arranged in irregular rows.

The main terminal armature consists of a row of very long, straight, evenly tapered bipinnate bristles extending from the distal edge of the membrane right round the tip. In addition, on the outer surface 5 or 6 short subterminal bristles or hairs are visible.

Edmondson's figures (1954, fig. 7*c,d*) do not show the membrane and are barely recognizable.

The pleopod shows marked resemblances to that of *L. polybiodes* Adams & White (see Stephenson and Campbell 1960, figs. 1*F* and 2*H*) but differs in being more curved, having a relatively shorter membrane, a relatively more slender tip, and in possessing short subterminal bristles on the outer surface. The pleopod of *L. laevis* (see Fig. 1*C*) is markedly different.

*Comments*

Previous Australian records are from Murray Island (Calman 1900) and Moreton Bay (Stephenson and Campbell 1960) both in Queensland.

## Subfamily **PORTUNINAE** Stephenson & Campbell

## Genus LUPOCYCLUS Adams & White

### Lupocyclus rotundatus Adams & White

Fig. 3*B*

*Lupocyclus rotundatus* Adams and White, 1849, p. 47, pl. xii, fig. 4. Stephenson and Campbell, 1960, pp. 108–11, figs. 1*K*, 2*M*; pl. 4, fig. 3; pl. 5*M*.

*Material Examined*

WESTERN AUSTRALIA: ♀ (24 mm) 3–4 miles off E. end Delambre I. Dampier Arch., B. R. Wilson, 5.vi.1960, dredged 10 fm (W. Aust. Mus. Reg. No. 54–60); ♀ (24 mm) Gidley I. Dampier Arch., R. D. Royce, 1.vi.1960, dredged 10 fm coral rubble (W. Aust. Mus. Reg. No. 55–60); ♂ (20 mm) 5 or 6 miles off Bazout I. Dampier Arch., B. R. Wilson, 5.vi.1960, dredged 23 fm sand (W. Aust. Mus. Reg. No. 56–60); 2 juveniles (8·8, 9·6 mm) W. approaches to Mermaid Straight, R. D. Royce, 27.v.1960, dredged 20 fm coral and sand (W. Aust. Mus. Reg. 57–60); ♀ (29 mm) between Onslow and Port Sampson, B. R. Wilson, June 1960, dredged (W. Aust. Mus. Reg. No. 58–60); ♀ (16 mm) 30 miles off Dampier Arch., R. D. Royce, 2.vi.1960, dredged 31 fm sand (W. Aust. Mus. Reg. No. 60–60); ♂ (23 mm) NE. Malus I., Dampier Arch, R. D. Royce, 31.v.1960, dredged 10 fm (W. Aust. Mus. Reg. No. 67–60).

*Material illustrated.*—Male pleopod, specimen 67–60 above.

*Comments*

The above specimens differ from the large males collected in Queensland which were previously described (Stephenson and Campbell 1960) as follows:

(1) The length/breadth ratio is from 85–87/100 for the five larger specimens, but 94–95/100 for the three smaller ones.

(2) The conspicuousness of the groove separating the lateral frontal teeth from the inner orbital lobes varies from being inconspicuous in the smaller specimens and also in the males to being deep and distinct in the three large females.

(3) The appearance of the metagastric ridges also varies, these lying transversely in the two juvenile specimens but exhibiting some degree of a broad posteriorly directed V-shape in the remainder.

(4) The male pleopods differ in minor respects in that the subterminal bristles on the inner side are somewhat larger, approximating in size to the stout, blunt conical spines on the upper surface. In addition, in specimen 56–60, only one such spine is present on the upper surface and in 67–60 three (see fig. 3*B*).

(5) The chelipeds are relatively shorter with the ratio of length of cheliped to carapace breadth in the present specimens being 2–2¼.

(6) The spinulation of the wrist. In the present specimens each wrist bears three spines with the two on the outer surface being approximately equal in size. In the Queensland specimens three spines are present and the past description was inaccurate in this respect. However, the upper spine on the outer surface is much smaller than the other two.

Collectively these differences do not justify separation at the specific level and much larger collections would be required before subspecific categories could be erected with any degree of certainty.

Features (2) and (3) above were used, with others, to separate *L. rotundatus* from *L. inaequalis* (Walker, 1887) (Stephenson and Campbell 1960, pp. 108–9). However, the two species are quite separate and the present species differs from Leene's (1940, pl. 1) figure of *L. rotundatus* = *L. inaequalis* in the following respects not previously listed:

(1) The anterior mesobranchials, a rounded patch of granules instead of a granular line.

(2) Cardiacs similarly a rounded patch of granules instead of a granular line.

(3) Median postcardiac a small granular patch instead of a broad granular line.

The species was not previously known from Western Australia.

### Lupocyclus tugelae Barnard

Figs. 1*E*, 3*C*; Plate 2, Fig. 1

*Lupocyclus tugelae* Barnard, 1950, p. 148, fig. 29*e–h*.

*Material Examined*

WESTERN AUSTRALIA: ♂ (9 mm) 7–8 miles N. of Long I. near Onslow, B. R. Wilson, 17.vi.1960, dredged 28 fm sand and sponge (W. Aust. Mus. Reg. No. 104–60); ♀ (13 mm) 25 miles NW. Angel I. Dampier Arch., R. D. Royce, 2.vi.1960, dredged 37 fm (W. Aust. Mus. Reg. No. 53(*a*)–60); ♀ (11 mm) data as above (W. Aust. Mus. Reg. No. 53(*b*)–60); ♀ (10·5 mm) (ovigerous) 3 miles NNW. of Anchor I., near Onslow, B. R. Wilson, 17.vi.1960, dredged 22 fm (W. Aust. Mus. Reg. No. 59–60).

*Material illustrated.*—Male pleopod and abdomen: specimen 104–60; general dorsal view: specimen 53(*a*)–60.

*Description*

*Front.*—Protruding with 4 teeth, the medians triangular, the laterals obtuse and clearly separated from the inner supraorbital lobes.

*Anterolateral teeth.*—Five large teeth alternating with 4 smaller ones. The first tooth is stout and blunt and the 4 remaining larger teeth are sharp and curved to point forwards, the last being the most protruding. The 4 smaller teeth are in the form of rounded lobes and of these, often the third is barely recognizable; sometimes this also applies to second and fourth.

*Carapace.*—Broader than long, length 77–83% of breadth, bearing a fine dense pile through which the following main granular areas are visible: frontal region, a diffuse band of small granules extending back almost to the protogastrics; frontals ill-developed; protogastrics each a broad patch; mesogastrics of each side formed of two separate conspicuous, elevated, granular regions almost tubercular in appearance; metagastrics a pair of short markedly elevated granular regions broadly separate in the mid-line; cardiacs a similar pair of elevated granular tubercles; median postcardiacs similar but small. The anterolaterals form a broad band extending from

first to third of the (larger) anterolateral teeth and passing inwards to the region of the mesogastrics. A small but diffuse cluster of granules lying posterolateral to the protogastrics may be either a continuation of them, or a portion of the mesogastric series, or a continuation of the anterolaterals. Epibranchials short, distinct, and sometimes ending mesially in a short tubercle-like cluster. Three mesobranchials of which the anterior, lying in prolongation of the line of the epibranchials, is a discrete sharply elevated tubercle, the median is also tubercular, and the posterior forms a short granular ridge.

*Chelipeds*.—Moderately elongate, about 2–2¼ times the length of the carapace. Anterior border of the arm bearing 5 spines which distally become larger and more widely spaced; posterior border with 2 spines, one at the distal end and one three-quarters of the way along the appendage. Wrist with 2 spines. Hand with 3 spines (and sometimes in addition a spiniform tubercle at its antero-external distal extremity) and 6 granular carinae, those bounding the lower surface being somewhat indistinct. Fingers grooved and approximately the length of the palm.

*First male pleopod* (based on a single specimen).—Smoothly and sharply curving to a non-flared acute tip. Beyond the basal lobes on the outer side, apart from occasional microscopic spinules, bare to and including the tip with no terminal armature visible in profile view. The inner surface is bare up to the subterminal armature, which consists of 6 stout, blunt, conical, backwardly directed spines. On the upper surface, there are 2 further blunt conical spines together with about 15 short backwardly directed spinules arranged in an irregular row. About 10 such spinules, irregularly arranged, are present on the under surface.

*Comments*

This species differs conspicuously from all others in the genus by possessing granular clusters instead of ridges on the dorsal surface of the carapace. The present material differs from Barnard's only in:

(1) The form of the granulation of the epibranchial ridge of the carapace. Barnard figures evenly spaced granules which he describes as "pointing forwards and appearing as elongate granules".

(2) The form of the metagastric ornamentation. Barnard does not describe the lateral granular clusters shown clearly on the present material, nor do they appear on his figure.

(3) The form of the front. In the present species, inner orbital lobes, lateral frontal lobes, and median frontal lobes are more confluent than shown on Barnard's figures.

Barnard's description is based upon a single incomplete female and until topotypical males can be obtained there must be some uncertainty regarding the present identification.

*Distribution*

Previously known only from 36 fm off Tugela River mouth, South Africa.

## Genus PORTUNUS Weber

### Portunus argentatus (A. Milne Edwards)

Figs. 1*F*, 3*D*; Plate 2, Fig. 2; Plates 4*D*, 5*A*

*Amphitrite argentata* White, 1847, p. 146 (descriptio nulla).
*Neptunus argentatus* (White). Milne Edwards, A., 1861, pp. 332, 339, pl. xxxi, figs. 4, 4*a*, 4*b*. Henderson, 1893, p. 368.
*Neptunus* (*Amphitrite*) *gladiator*, var. *argentatus* (White). Miers, 1886, pp. 177–8. Cano, 1889, p. 214. Ortmann, 1893, p. 73 (fide Alcock 1899).
*Neptunus* (*Amphitrite*) *argentatus* (White). Alcock, 1899, pp. 36–7. Laurie, 1906, p. 413. Sakai, 1939, p. 391, fig. 5*b*, pl. lxxxi, fig. 1.
*Portunus* (*Achelous*) *argentatus* (Milne Edwards). Rathbun, 1906, p. 871. Edmondson, 1954, pp. 238–9, figs. 14, 15.
*Monomia argentata* (White, Milne Edwards). Barnard, 1950, pp. 156–8, figs. 27*c*, 30*a–d*.

*Material Examined*

WESTERN AUSTRALIA: ♂ (22 mm) 7–8 miles N. of Long I. near Onslow, B. R. Wilson, 17.vi.1960, dredged sand and sponge, 28 fm (W. Aust. Mus. Reg. No. 68–60); ♀ (23 mm) 25 miles NW. of Angel I., Dampier Arch., R. D. Royce, 2.vi.1960, dredged 37 fm (W. Aust. Mus. Reg. No. 79–60).

*Material illustrated.*—Dorsal view and third maxilliped: female above; male abdomen and pleopod: male above.

*Description*

*Front.*—Four-lobed, all lobes rounded and low, the laterals being not quite twice the breadth of the medians. The upper border of the orbit bears a distinct tooth and a similar tooth is present on the median side of the lower border of the orbit, close to the basal antennal joint.

*Anterolateral teeth.*—The first relatively large and blunt, the next seven of increasing sharpness, the last distinctly the largest and projecting directly outwards.

*Carapace.*—Relatively broad (breadth *c.* 1·8 times length). Anterolateral borders forming a curve whose centre lies in the cardiac region. Posterior–posterolateral junction rounded and with a small right-angled projection on a lower plane. Surface covered with widely spaced conspicuous granulated areas separated by regions covered by a dense pubescence. Frontals lie a little behind the elevated border; the orbitals lie on this border; protogastrics large; a narrow band running through mesogastrics to metagastrics, the latter having a distinct anterior termination; 2 cardiacs and 3 postcardiacs; anterolaterals well developed; epibranchials distinct and with scattered granules anterior to them; three mesobranchials; posterolaterals distinct. Posterior border of carapace finely beaded.

*Chelipeds.*—Pubescent and with squamiform granules. Posterodistal border of the arm bearing 2 sharp spines. Anterior border of the arm bearing 4 spines or 3 spines and a spiniform tubercle. Wrist with 2 usual spines. Upper surface of the arm with the 3 usual carinae, all granular but only the innermost ending in a spine. Outer surface of hand with very distinct carina, inner surface with indistinct carina. Fingers sharp and strongly carinated.

*Fifth leg.*—Posterodistal border of merus finely serrated. A conspicuous purplish red spot on the distal end of the dactylus.

*Third maxilliped.*—Antero-external angle of merus strongly produced in a lateral direction.

*Male abdomen.*—Ultimate segment roundly triangular, penultimate segment with convex sides, slightly longer than broad (1·2 times).

*First male pleopod* (based on one specimen).—Short, stout, sharply curved, swollen distally, and with the tip bearing a membrane. Beyond the basal lobes the outer surface is bare apart from the terminal armature. The inner surface bears a short series of bipinnate hairs about a fifth of the distance up the appendage, thereafter is bare to the terminal armature. Terminal armature complex. On the outer surface in profile view, there is only a single spinule, whereas on the inner surface, approximately 40 elongate bristles are visible. These are slightly forwardly directed, being proximal to the membrane and at the level of the membrane form irregular transverse rows both above and below the membrane. On the upper surface, there is an elongate scattered patch of approximately 15 short, stout, forwardly directed bristles. On the under surface, the elongate bristles form a broad patch towards the inner surface, while towards the outer surface there is an irregular double row of minute backwardly directed spinules.

*Colour.*—After 2 months in alcohol, there are orange-red spots on the upper surface of the chelae and diffuse blotches on the walking legs. Fifth leg with a purplish red spot on the distal half of the dactylus. Carapace granules pale to deep red-orange. When the surface of the specimens has partially dried a beautiful mother-of-pearl lustre appears on the immovable finger, the outer carina of the hand, the outer spine of the wrist, the antennae and antennules, and the abdominal carinae.

*Comments*

Edmondson's (1954) figure of the male abdomen (fig. 14*b*) resembles that of the present specimens but his figures (figs. 14*c*,*d*) of the male pleopod are barely recognizable.

*Distribution*

Not previously recorded from Australia but known from Natal, Zanzibar, and the Red Sea to Polynesia (fide Sakai 1939 and Barnard 1950).

### Portunus curvipenis, sp. nov.

Figs. 1*G*, 3*E*; Plate 2, Fig. 3; Plates 4*E*, 5*B*

*Material Examined and Illustrated*

WESTERN AUSTRALIA: ♂ holotype (52 mm) Exmouth Gulf, W. and W. Poole, Oct.–Nov. 1958, trawled (W. Aust. Mus. Reg. No. 6–60).

*Description*

*Front.*—Four-lobed, the two medians distinct and acute, the laterals almost right-angled and much broader.

*Anterolateral teeth.*—Approximately of equal size, the first broad and blunt, the next seven subequal, the last distinctly the broadest and most protruding.

*Carapace.*—Moderately narrow (breadth 1·65 times length). Anterolateral borders form an arc whose centre lies just behind the cardiac region. Posterior–posterolateral junction rounded and with a rounded projection on a lower plane. Surface covered with widely spaced very conspicuously granulated areas, these being separated by pubescent regions. Frontals inconspicuous consisting of about 4 small granules; orbitals lying on orbital border; protogastrics confluent with the mesogastric, whose anterior border almost forms a granulated ridge; metagastric region occupied by a continuous band; a pair of cardiacs; 3 distinct postcardiacs all continuing further towards the posterior border of the carapace than in *P. rubromarginatus;* anterolaterals well developed; epibranchials somewhat diffuse; mesobranchial consisting of 3 distinct patches; posterolaterals small; posterior border of carapace finely beaded.

*Chelipeds.*—Pubescent and with squamiform granulation. Posterodistal border of arm with 2 spines, the more distal marking the position of a very indistinctly beaded carina. Anterior border of the arm with 4 spines. Wrist with the 2 usual spines. Upper surface of the hand with the 3 usual carinae (these being less distinctly granular than in *P. rubromarginatus*) and only the innermost ending in a spine (apparently broken from the left cheliped). Carina on the outer surface very distinct but not granular, that on the inner surface granular and tolerably recognizable.

*Fifth leg.*—Posterodistal border of the merus ending in 2 spinules followed by a finely serrated region.

*Third maxilliped.*—Antero-external angle of merus hardly produced in a lateral direction.

*Male abdomen.*—Ultimate segment elongate and lanceolate. Penultimate segment also elongate.

*First male pleopod* (based on a single specimen).—Elongate and curved with a distinct change in curvature near the middle, leading to a fine but blunt tip curved distinctly outwards. Beyond the basal lobes about half the outer surface is covered by moderately long bipinnate hairs followed by an apparently bare area. At roughly the centre of this area and at the point of change of curvature there is a dense patch of rounded spinules which are directed in a slightly backwards direction. On the inner surface beyond the basal lobes there are again bipinnate hairs which extend about one-fifth of the distance up the appendage, followed by a bare area apparently extending to the tip. A few distantly spaced microscopic spinules are actually present on the outer surface of the distal one-fifth of the appendage. These comprise the only terminal armature visible from the upper surface. On the under surface numerous spinules are present particularly towards the outer edge of the appendage, these continuing down the appendage to merge with the dense patch of spinules visible near the middle of the outer side.

The pleopod resembles that of *P. rubromarginatus* in its general shape and in possessing a cluster of spinules halfway up the appendage on the outer side. It differs in the more abrupt change of curvature near the middle, in the curvature

at the tip, and in the details of spinulation on the under surface of the tip (compare with Stephenson and Campbell 1959, figs. 2*K*, 3*K*).

*Colour*.—After 6 months in alcohol the only distinctive colour is pale pink on the spines on the anterior border of the arm and pale orange-red on numerous carapace granules.

*Comments*

The species bears a remarkable general resemblance to *P. rubromarginatus*, differing from it conspicuously in:

(1) having two spines on the posterior border of the arm of the cheliped, not one;
(2) having the antero-external angle of the merus barely produced instead of distinctly produced in a lateral direction;
(3) the tip of the male pleopod being sharply curved outwards;
(4) the details of granulation of the carapace, particularly on the mesogastric and mesobranchial regions.

In the key (Stephenson and Campbell 1959, p. 90) the species keys out with *P. pubescens* (Dana) and *P. oahuensis* Edmondson, but differs conspicuously from both in having the carapace surface covered by conspicuous granulated areas instead of transverse ridges or tubercles respectively.

### Portunus granulatus (H. Milne Edwards)

*Portunus granulatus* (Milne Edwards, H.). Stephenson and Campbell, 1959, pp. 108–10, figs. 2*I*, 3*I*, pl. 3, fig. 1*E*, pls. 4*I*, 5*I*.

*Material Examined*

WESTERN AUSTRALIA: Six specimens from Maud Landing, Shark Bay, Gidley I. Dampier Arch. (specimens in W. Aust. Mus.) QUEENSLAND: ♂ (31 mm) N. side Heron I., 7.xi.1960, coll. W.S., in 5 cm of water at half-ebbed tide, reef flat, sandy coral gravel.

*Comments*

After 2 months in alcohol the Western Australian specimens show evidences of natural colouring as follows: confused dark mottling in the anterior half of the carapace particularly outlining the gastric regions; dark blotches in the central cardiac and postcardiac regions; a minority of carapace granules orange-red in colour.

The Queensland specimen, the largest obtained in Australia, is from the shallowest habitat recorded. The colour alive was pale cream, with a minority of carapace granules dark brown.

### Portunus orbitosinus Rathbun

*Portunus orbitosinus* Rathbun. Stephenson and Campbell, 1959, pp. 113–4, figs. 2*L*, 3*L*; pl. 3, fig. 4; pls. 4*L*, 5*L*.

*Material Examined*

WESTERN AUSTRALIA: ♂ (14 mm) 4 miles W. of Cape St. Cricq, Dorre I., Shark Bay, R. W. George, 16.v.1960, dredged 40 fm (W. Aust. Mus. Reg. No. 47*a*–60);

♀ (17 mm), ♂ (11 mm) 4 miles SW. of Cape Ronsard and Bernier I., R. W. George, 16.v.1960, dredged 30 fm sand and weed (W. Aust. Mus. Reg. No. 49–60); ♀ (22 mm) 20 miles off Delambre I., Dampier Arch., B. R. Wilson, 7.vi.1960, dredged 23 fm (W. Aust. Mus. Reg. No. 73–60); ♀ (ovigerous) (16 mm) 7–8 miles N. of Long I. near Onslow, B. R. Wilson, 17.vi.1960, dredged 28 fm sand and sponge (W. Aust. Mus. Reg. No. 74–60); ♀ (ovigerous) (*c.* 18 mm) 5 miles offshore N. of Maud Landing, R. D. Royce, 2.v.1960, dredged 31 fm, coral rubble (W. Aust. Mus. Reg. No. 75–60); ♂ (18 mm) 25 miles NW. of Angel I., Dampier Arch., R. D. Royce, 2.vi.1960, dredged 37 fm (W. Aust. Mus. Reg. No. 77–60); ♂ (25 mm) 5–6 miles off Bezout I., Dampier Arch., B. R. Wilson, 5.vi.1960, dredged 23 fm (W. Aust. Mus. Reg. No. 87–60); ♀ (17 mm) between Onslow and Pt. Sampson, B. R. Wilson, June 1960, dredged (W. Aust. Mus. Reg. No. 88–60); ♂ (23 mm) 30 miles N. of Dampier Arch., R. D. Royce, 2.vi.1960, dredged 31 fm (W. Aust. Mus. Reg. No. 91–60).

*Comments*

Previously only a single Queensland specimen was known from Australia and the present records are hence new to Western Australia.

After a month in alcohol the specimens show evidences of natural colouring as follows: a minority of the granules in each of the main regions and typically outlining these regions a deep orange-red or blood-red; similar red granules on the chelipeds, and red blotches on most of the segments of the remaining legs.

### Portunus pseudoargentatus, sp. nov.

Figs. 2*A*, 3*F*; Plate 2, Fig. 4; Plates 4*F*, 5*D*

*Material Examined and Illustrated*

WESTERN AUSTRALIA: ♂ holotype (63 mm) 5 miles NW. of Gun I., southern group Abrolhos Is., R. W. George, 11.v.1960, dredged coral rubble, sponge, seaweed, 30–35 fm (W. Aust. Mus. Reg. No. 50–60) (no legs present on right side).

*Description*

*Front.*—Four-lobed, all lobes rounded and distinct, the laterals about twice the width of the medians. The upper border of the orbit is marked by a distinct and prominent tooth and a similar tooth is present on the median side of the lower border of the orbit close to the basal antennal joint.

*Anterolateral teeth.*—The first relatively large and blunt, the next seven sharp and of progressively increasing size and directed forwards, the last distinctly the largest and projecting directly outwards.

*Carapace.*—Relatively broad (breadth 1·8 times length). Anterolateral borders forming a broad curve whose centre lies in the postcardiac region. Posterior–postero-lateral junction rounded and with a small right-angled projection on a lower plane. Surface covered with widely spaced conspicuous granulated areas separated by regions covered by a dense pubescence. Frontals lie a little behind the elevated border; the orbitals lie on this border; protogastrics diffuse; a narrow band running through mesogastrics to metagastrics, the latter having a distinct anterior termination; two cardiacs and three postcardiacs; anterolaterals well developed;

epibranchials distinct and with scattered granules anterior to them; 3 mesobranchials; diffuse posterolaterals. Posterior border of carapace finely beaded.

*Chelipeds.*—Pubescent and with squamiform granules. Posterodistal border of the arm bearing 2 sharp spines, the proximal terminating a beaded carina. Anterior border of the arm with 4 spines. Wrist with 2 usual spines. Upper surface of the arm with the 3 usual carinae, all granular but only the innermost ending in a spine. Outer surface of hand with very distinct carina, inner surface with carina less distinct but recognizable. Fingers sharp and strongly carinated.

*Fifth leg.*—Posterodistal border of merus finely serrated. A conspicuous purplish red spot on the distal end of the propodus.

*Third maxilliped.*—Antero-external angle of merus strongly produced in a lateral direction.

*Male abdomen.*—Ultimate segment roundly triangular, penultimate segment parallel-sided in its proximal half, 1½ times as long as broad.

*First male pleopod.*—Elongate and sharply curved with an almost right-angled bend in the middle. Proximal half relatively thin, tip slightly spooned. Beyond the basal lobes, the outer surface is bare apart from the terminal armature. The inner surface bears bipinnate hairs on the distal one-fifth of the appendage. Two or three inconspicuous spinules are present near the centre of the inner surface, otherwise it is likewise bare up to the terminal armature. Terminal armature: on the outer side 4 stout spinules are visible in lateral view, on the inner side approximately 12. On the upper surface there is a double row of spinules towards the outer side with approximately 24 visible. On the under surface the sparse band of spinules (approx. 12 in number) runs between those of the outer and inner sides.

*Colour.*—After 2 months in alcohol, there are reddish orange markings on the arm, hand, and finger of the chelipeds, on the metagastric and epibranchial regions of the carapace, in addition to the conspicuous purplish red mark on the propodus of the fifth leg.

*Comments*

This species shows general resemblances to *P. argentatus*, *P. rubromarginatus*, *P. gladiator*, and *P. curvipenis*. It differs from *P. rubromarginatus* in possessing two spines on the posterior border of the arm and from both *P. gladiator* and *P. curvipenis* in the form of the male abdomen and pleopod. It is closest to *P. argentatus* but differs from it in being a larger species, in the more protruding frontal teeth, the more conspicuous dentiform process on the upper border of the orbit, in having a black area on the propodus of the fifth leg instead of on the dactylus (this enables the species to be separated in Stephenson's and Campbell's key (1959, p. 90)), in having a more parallel-sided male abdomen, in the form of the male pleopods, and because it lacks the characteristic pearly sheen of *P. argentatus*.

It should be noted that Milne Edwards's (1861) original description of White's types of *P. argentatus* figures a male abdomen identical with the present species, and omits to mention the pearly lustre. It is impossible to distinguish *P. argentatus* from the present species on the basis of Milne Edwards's description.

The mention of the spot on the dactylus (Miers 1886 and subsequent workers) and the presence of the pearly sheen on the holotype of *P. argentatus* (Henderson 1893 and subsequent workers) suggests that Milne Edwards figure of the male abdomen of *P. argentatus* was inaccurate.

### Portunus pubescens (Dana)

*Portunus pubescens* (Dana). Stephenson and Campbell, 1960, pp. 99–101; figs. 2*C*, 3*C*, pl. 1, fig. 3, pls. 4*C*, 5*C*.

*Material Examined*

WESTERN AUSTRALIA: Leighton Beach, L. Glauert, May 1928. (W. Aus. Mus. Reg. No. 13445—dried specimen); ♂ (25 mm), ♀ (31 mm) Maud Landing, R. D. Royce, 20.v.1960, dredged 10 fm, sand, weed, and rock (W. Aust. Mus. Reg. No. 83–60).

*Comments*

New records for Western Australia and apparently for the Indian Ocean.

### Portunus rugosus (A. Milne Edwards)

Figs. 2*B*, 3*G*; Plate 3, Fig. 1; Plates 4*G*, 5*E*

*Neptunus rugosus* Milne Edwards, A., 1861, p. 335, pl. xxxiii, fig. 3. Hess, 1865, p. 139. Milne Edwards, A., 1873, pp. 156–7. Miers, 1886, pp. 176–7 (partim). Man, 1887, pp. 70–3 (under *N. andersoni*). Henderson, 1893, p. 369 (under *N. andersoni*).
*Portunus rugosus* (Milne Edwards, A.). Guinot, 1957, p. 480 (under *P. mariei*).

*Material Examined*

WESTERN AUSTRALIA: ♂ (24 mm) 2 miles off Cottesloe, 4 fm, R. W. George, 5.v.1960 (W. Aust. Mus. Reg. No. 46–60); 2 ♂♂ (14, 23 mm), 5 ♀♀ (21–24 mm), NE. side Dirk Hartog I., R. W. George, 15.v.1960, dip net at night (W. Aust. Mus. Reg. No. 47–60); ♀ (30 mm), ♀ (31 mm) E. side of Dirk Hartog I., Shark Bay, R. W. George, 15.v.1960, dredged 7 fm sand (W. Aust. Mus. Reg. No. 51–60).

*Material illustrated.*—The 30-mm specimen.

*Discussion of the Species*

Milne Edwards's original description is as follows:

"Carapace très-fortement bosselée, les parties saillantes granuleuses, les parties rentrantes lisses. Bords latéro-antérieurs garnis de dents très-petites et dirigées en avant. Cornes latérales très-grandes, très-minces et légèrement dirigées en arrière. Angles postérieurs de la carapace aigus et spiniformes. Front à cinq dents, la médiane pointue et un peu plus courte que les mitoyennes, les externes courtes et obtuses. Orbites très-profondes. Yeux très-gros. Apophyse épistomienne ne dépassant pas le front. Pattes antérieures courtes. Bras portant trois épines sur son bord antérieur et une à l'extrémité de son bord postérieur. Avant-bras à deux épines, l'une à l'angle antéro-interne, l'autre sur la face externe. Main armée de deux épines, l'une au-dessus de l'articulation de l'avant-bras, l'autre au-dessus de la base du pouce. Pattes suivantes grêles. Abdomen du mâle triangulaire et à bords sinueux.

Largeur de la carapace, $0^{m}$, 035; longeur, $0^{m}$, 016.

Habitation.—Australie.

Cette espèce, qui se rapproche, par la forme de la carapace terminée en arrière par des angles spiniformes, des *N. hastatoides* et *N. tuberculosus*, s'en distingue par un caractère de premier ordre tiré de la disposition du front découpé en cinq dents dont une médiane. C'est de tous les Neptunes, à l'exception du *N. tenuipes*, le seul qui présente cette particularité."

The only additional important comment in the literature is in Miers (1886) who notes that Milne Edwards's material was from Shark Bay, Western Australia, and who also records a small male from Torres Strait, an adult male (breadth 23·5 mm) from the Philippines, and a female from the Celebes Sea. He notes that the Philippines and the Celebes Sea specimens differ from Milne Edwards's "by the much less strongly and distinctly tuberculated carapace, the much shorter epibranchial spine, and the longer chelipeds, distinctions which are supposed to be due to the greater age of the Challenger specimens". He further notes that these specimens more nearly resemble *P. tenuipes* than *P. rugosus* except for the dentiform posterolateral angles of the carapace. Since the present material includes larger specimens than Miers examined and since all possess strongly tuberculated carapaces and long epibranchial spines, it seems probable that the Philippines and Celebes specimens of Miers should be referred to another species.

Apparently the species has not been redescribed nor have any additional comments upon its structure been given. For complete certainty in identification of the present specimens it would be necessary to examine Milne Edwards's original material since his description excludes important features such as the form of merus of the third maxilliped, and the detailed shape of the male abdomen and the male pleopod.

*Description*

*Front.*—Three-toothed, with all teeth sharp and somewhat projecting, the laterals broader than the median.

*Anterolateral teeth.*—The first broad and blunt, the next seven increasing in sharpness, the last much the longest and directed slightly backwards. The fourth, sixth, and eighth teeth are noticeably smaller than the third, fifth, and seventh in all the present specimens. This point is not mentioned in Milne Edwards's description nor is it shown on his figures.

*Carapace.*—Broad (breadth 2·1–2·2 times length) with large orbits and conspicuous elevated granular patches separated by areas with a dense pubescence. Anterolateral borders form a curve whose centre lies just behind the cardiac region. Posterior–posterolateral junction elevated to form a short ridge bearing an almost right-angled border. (Milne Edwards described these angles as "aigus et spiniformes" and figures them as definitely acute.)

Of the granulated areas of the carapace, frontals and orbitals are sometimes absent but the remainder are present and conspicuous and include a pair of post-frontals. Protogastric regions each typically bearing 2 almost separate patches of granules. These are sometimes fused as shown in Milne Edwards's figures. There are 3 separate patches in the mesogastric region and 2 in the metagastric. A pair of cardiacs and 3 postcardiacs are present. The anterolaterals consist of a discrete pair on either side. Epibranchials short and discrete. Three mesobranchials, the most posterior forming almost a ridge. Posterolaterals short and again ridge-like.

*Chelipeds.*—Elongate, the right stouter than the left. Upper surface microscopically granular and bearing long hairs on the borders of many of the segments; lower surface with squamiform markings. Posterodistal border of the arm bearing a single sharp spine, anterior border with 3 such spines. Wrist with the usual spines but with carinae ill-developed. Upper surface of the hand bearing a conspicuous inner carina which terminates in a spine; a distinct outer carina typically granular, and a central less well-developed granular carina. The outer surface of the hand bears a central granular carina; the inner and under surfaces bear well-developed squamiform markings.

*Fifth leg.*—Posterodistal border of merus finely serrated.

*Third maxilliped.*—Antero-external angle of merus with a flattened expansion directed more forwards than laterally.

*Male abdomen.*—Penultimate segment approximately as long as broad and with gradually convergent or even slightly concave borders. Ultimate segment heart-shaped.

*First male pleopod* (based on three specimens).—Short, stout, moderately strongly curved. Beyond the basal lobes on the outer side bare for about half the way up the appendage, thereafter short backwardly directed spinules continue almost to the tip. On the inner surface, a single row of regularly arranged, distantly spaced, forwardly directed, bipinnate hairs are present on some specimens near the middle of the appendage. These decrease in size distally to become spiniform, and are followed by backwardly directed subterminal spinules. The terminal armature consists of these spinules which form a series of irregular curved rows on the under surface, and which continue round the sides to appear on each side of the upper surface. Approximately 20 spinules are visible in profile view on the outer side and 3–15 on the inner.

*Comments*

This species, which was not present in any of the more recent Australian collections, was overlooked by Haswell (1882) in his catalogue, and also by Stephenson and Campbell (1959).

It resembles *P. tenuipes* in general facies and keys out with this species or *P. mariei* in Stephenson and Campbell (1959, p. 90). It differs from *P. tenuipes* in:

(1) the form of the lateral frontal teeth which in *P. tenuipes* are much broader than the medians and relatively rounded;

(2) the much more elevated and conspicuous granular eminences in the carapace;

(3) the ultimate segment of the male abdomen which in *P. tenuipes* is more rounded;

(4) the details of spinulation of the male pleopod.

It also differs conspicuously from *P. mariei* in:

(1) the conspicuous granular eminences on the carapace;

(2) the posterodistal border of the arm with a single spine instead of two.

The only points of disagreement with Milne Edwards's original description and figures are:

(1) the alternation between larger and smaller anterolateral teeth;

(2) the less acute posterior–posterolateral junction of the carapace.

*Distribution*

Australia (Milne Edwards 1861), New Caledonia (Milne Edwards 1873), Torres Strait (Miers 1886).

PORTUNUS TENUICAUDATUS, sp. nov.

Figs. 2*C*, 3*H*; Plate 3, Fig. 2; Plates 4*H*, 5*C*

*Material Examined*

WESTERN AUSTRALIA: ♂ holotype (14 mm) 30 miles N. of Dampier Arch., R. D. Royce, 2.vi.1960, dredged 31 fm sand (W. Aust. Mus. Reg. No. 62(*b*)–60); ♀ allotype (12 mm) 5 miles offshore N. of Maud Landing, R. D. Royce, 2.v.1960 (W. Aust. Mus. Reg. No. 75(*b*)–60).

*Material illustrated.*—Holotype.

*Description*

*Front.*—Four-lobed, the medians low-set, rounded, and small, and the laterals very much broader, considerably projecting, and almost right-angled.

*Anterolateral teeth.*—Nine, of which the first is broad and blunt, the last very elongate and the remainder varying in length and sharpness, but with only the second, fourth, and sixth of normal (i.e. large) size.

*Carapace.*—Very broad (breadth 2–2½ times length). The anterolateral borders, excluding the ninth tooth, form a fairly narrow arc whose centre lies in the cardiac region. Posterior–posterolateral junction an elevated region with an angle of approximately 90°. Carapace with elevated granular areas separated by pubescent regions and with characteristic, conspicuous elevated portions of almost spiniform structure.

These are situated as follows: one on each protogastric region, single median one just anterior to mesogastric region, a pair on the cardiac, a single one in the median postcardiac region, and one in the centre of each mesobranchial area. In addition the following normal granular patches are present: protogastrics (broadly separated anteriorly), discrete mesogastrics, short ridge-like metagastrics, cardiacs, lateral postcardiacs (each in the form of 2 irregular oblique rows of granules), anterolaterals each as 2 discrete patches, broad epibranchials, 3 pairs of mesobranchials, and short elevated posterolaterals.

*Chelipeds.*—Unequal, the right slightly larger than the left. Elongate, hairy, and granular. Posterodistal border of the arm with a spine or spiniform tubercle, anterior border with 3 or 4 spines. Wrist with the 2 usual spines, the outermost marking the end of a conspicuous carina. A second carina is present on the upper, outer surface but is conspicuous only in the male. Upper surface of hand broad and bearing 3 low carinae of which the innermost ends in a spine and the middle in a spiniform tubercle. Outer surface of hand of larger chela bearing low but distinguishable carinae, whereas these carinae are acute and distinct in the smaller cheliped. Under surface of hand finely granular.

*Fifth leg.*—Posterior and posterodistal border of merus granular.

*Third maxilliped.*—Antero-external angle of merus produced forwards.

*Male abdomen.*—Penultimate segment longer than broad, with markedly concave lateral borders and with a thin distal half (hence the specific name). Ultimate segment about two-thirds length of the penultimate and itself about two-thirds as broad as long.

*First male pleopod* (based on one specimen).—Short and robust, with a general shape resembling *P. longispinosus* and *P. emarginatus*. Inflated basely, then curving smoothly but sharply to a pointed tip. Beyond the basal lobes on the outer surface, bare to the tip apart from a single bristle about one-third of the distance along the appendage. Inner surface bearing elongate bipinnate hairs on the inflated basal portion, followed after an interval by 3 shorter bipinnate hairs about halfway up the appendage, and again bare to the terminal armature. Terminal bristles on the outer side: only 4 subterminal spinules visible in profile view. On the upper surface, there are 2 rows of similar spinules, one terminating well behind the tip and the other extending to the level of the terminal spinules of the outer side. Terminal bristles on the inner side: only 2 or 3 spinules visible subterminally in profile view, these representing the edges of a sparse subterminal patch. In addition, there is a row of small distantly spaced inconspicuous spinules on the inner side. On the under surface there are 2 indistinct lines of spinules running from side to side and a sparsely arranged row running somewhat towards the inner surface.

*Colour.*—In recently preserved specimens, the outline of the gastric region is marked in brownish pigment. In the male specimen additional brown areas are present showing some resemblance to the form of the human face.

*Comments*

This species keys out as *P. macrophthalmus* Rathbun in Stephenson and Campbell (1959, p. 89) and is very close to this species in the following respects:

(1) Irregularity in the anterolateral teeth.

(2) Concave borders of the penultimate segment of the male abdomen.

(3) Almost spiniform elevations on the carapace surface.

It differs from it as follows:

(1) Nine anterolateral teeth as against six or seven as mentioned by Rathbun (1906, p. 871) and Edmondson (1954, p. 242).

(2) Different relative lengths of penultimate and ultimate segments of the male abdomen. In *P. macrophthalmus* the ultimate segment is about four-tenths the length of the penultimate, whereas in the present species it is approximately two-thirds.

(3) Detailed ornamentation of the dorsal surface of the posterior half of the carapace. In *P. macrophthalmus* the cardiac and lateral postcardiac regions appear to be in the form of normal rounded, granular eminences (see Rathbun 1906, pl. xii, fig. 5) whereas in the present species, the cardiacs bear spiniform projections, while the lateral postcardiacs are each in the form of two irregular oblique rows of granules.

(4) Form of the male pleopods. In Edmondson's figure of *P. macrophthalmus* (Edmondson 1954, fig. 18*e*) this is shown as more sharply curved than in the present species.

## Genus CHARYBDIS de Haan

### Charybdis (Charybdis) callianassa (Herbst)

*Charybdis* (*Charybdis*) *callianassa* (Herbst). Leene, 1938, pp. 81–4, figs. 41–3. Stephenson, Hudson, and Campbell, 1957, pp. 493–5, figs. 1*B–D*, 2*C*, 3*D*, pl. 1, fig. 2, pl. 4*A*.

*Material Examined*

WESTERN AUSTRALIA: ♂ (37 mm) approx. 290 miles N. of Broome, 12° 58′ S., 121° 26′ E., *Umitaka Maru*, 23.xi.1960, dip net at 2100 hr using light at surface over about 200 fm (W. Aust. Mus. Reg. No. 357–60); 3 ♂♂ (39–41 mm), 5 ♀♀ (24–36 mm) 12° 58′ S., 120° 30′ E., *Umitaka Maru*, 24.xi.1960, stomach contents of "Big eye tuna" (W. Aust. Mus. Reg. No. 354–60).

Although the species is evidently common round the Australian coasts, no previous specimens have been obtained from comparable situations.

### Charybdis (Charybdis) miles de Haan

*Charybdis* (*Charybdis*) *miles* de Haan. Leene, 1938, pp. 38–42. figs. 10–13. Stephenson, Hudson, and Campbell, 1957, pp. 500–1, figs. 2*H*, 3*I*, pl. 2, fig. 3, pl. 4*F*.

*Material Examined*

WESTERN AUSTRALIA: ♀ (ovigerous) (59 mm), *c.* 80 miles N. of Roebourne, 19° 14′ S., 117° 18′ E., *Umitaka Maru*, 27.xi.60, otter trawled at 116–122 fm (W. Aust. Mus. Reg. No. 353–60).

Within Australia only known previously from New South Wales.

### Charybdis (Charybdis) jaubertensis Rathbun

*Charybdis* (*Charybdis*) *jaubertensis* Rathbun. Leene, 1938, pp. 67–8, fig. 31. Stephenson, Hudson, and Campbell, 1957, pp. 498, 500, figs. 2*A*, 3*A*, pl. 2, fig. 1, pl. 4*D*.

*Material Examined*

WESTERN AUSTRALIA: ♂ (19 mm) near bar of South Passage Shark Bay, R. W. George, 14.v.1960 (W. Aust. Mus. Reg. No. 36–60).

*Comments*

After a month in alcohol the specimen shows a characteristic pattern of blood-red markings as follows: (1) on the spine of the wrist, (2) on the two most distal spines on the anterior border of the arm, (3) one on each lateral end of the protogastric ridge of the carapace, (4) one on each lateral end of the metagastric ridge, (5) a pair on the cardiac region, and (6) a single larger one in each mesobranchial region. In addition to these, conspicuous orange-red markings are present on all carapace grooves. The lateral half of each third maxilliped is purple-red.

The separation of this species from *C. natator* (Herbst) in a previous key (Stephenson, Hudson, and Campbell 1957, p. 492) was by the bluntness of the last

four anterolateral teeth in *C. natator*. However, some specimens have sharp although stout teeth. A better separation is by carapace shape; in *C. jaubertensis* the carapace is long and the anterolateral borders are only a little inclined whereas in *C. natator* the carapace is broader and the anterolateral borders are sharply inclined. These differences are apparent from Plate 2 in Stephenson, Hudson, and Campbell (1957).

### Charybdis (Goniohellenus) truncata (Fabricius)

*Charybdis* (*Goniohellenus*) *truncata* (Fabricius). Leene, 1938, pp. 118–21, figs. 66, 67. Stephenson, Hudson, and Campbell, 1957, pp. 503–4, figs. 2*D*, 3*E*, pl. 3, fig. 3, pl. 4*I*.

*Material Examined*

WESTERN AUSTRALIA: ♀ (18 mm) 5 miles N. of Enderby I., Dampier Arch., R. D. Royce, 28.v.1960, dredged 22 fm fine sand (W. Aust. Mus. Reg. No. 66–60). ♂ (23 mm) approx. 14 miles NNW. of Anchor I. near Onslow, B. R. Wilson, 17.vi.1960. dredged 65 fm (W. Aust. Mus. Reg. No. 72–60). ♀ (17 mm) between Onslow and Pt. Sampson, B. R. Wilson, June 1960, dredged (W. Aust. Mus. Reg. No. 52–60).

*Comments*

Previously known in Western Australia only from Exmouth Gulf and not previously collected from deeper than 10 fm.

### Charybdis (Gonioneptunus) bimaculata (Miers)

*Charybdis* (*Gonioneptunus*) *bimaculata* (Miers). Leene, 1938, pp. 126–9, figs. 70–61. Stephenson, Hudson, and Campbell, 1957, pp. 504–5, figs. 2*J*, 3*K*, pl. 3, fig. 4, pls. 4*H*, 5*A*.

*Material Examined*

WESTERN AUSTRALIA: ♂ (30 mm), 90 miles NE. Barrow I., 19° 25′ S., 116° 25′ E., *Umitaka Maru*, 28.xi.1960, otter trawl (W. Aust. Mus. Reg. No. 355–60).

New record for Western Australia.

## Genus THALAMITA Latreille

### Thalamita admete (Herbst)

*Cancer admete* Herbst, 1803, pp. 40–1, pl. lvii, fig. 1.
*Thalamita savignyi* de Man, 1895, p. 564.
*Thalamita dispar* Rathbun, 1914, p. 657, pl. i, fig. 4.
*Thalamita admete* Stephenson and Hudson, 1957, pp. 320, 324–6, figs. 2*I*, 3*I*, pl. 1, fig. 1, pls. 7*A*, 10*A*.

Rathbun's (1914) paper was overlooked by Stephenson and Hudson (1957) with the result that the record of *T. dispar* from the Monte Bello Is. was omitted. The variability within *T. admete* is such as to include Rathbun's species.

Recent collections of *T. admete* in the Western Australian Museum are from Barrow I., Thevenard I., 15 miles NNW. of Onslow, near bar of South Passage Shark Bay, Pidgeon I., Wallabi Group, Abrolhos Is., Wreck Pt., Southern Group Abrolhos Is. The species has now been recorded, and is evidently common, both north and south of the Monte Bello Is.

### Thalamita dakini Montgomery

Figs. 2*D*, 3*J*; Plate 3, Fig. 3; Plates 4*I*, 5*F*

*Thalamita dakini* Montgomery, 1931, pp. 432–3, pl. 23, fig. 3; pl. 28, fig. 4. Stephenson and Hudson, 1957, pp. 334–5.

?*Thalamita medipacifica* Edmondson, 1954, pp. 260–2, figs. 34*a*,*b*, 35*a*.

This was the only Australian species of *Thalamita* not previously available in Australia, and hence not examined by Stephenson and Hudson (1957). A specimen was recently discovered by Dr. R. George amongst unsorted collections at the Western Australian Museum, and forms the basis of the revised description below.

*Material Examined and Illustrated*

WESTERN AUSTRALIA: ♂ 12 mm, Rottnest I., coll. children Rottnest State School, received 31.xii.1935 (W. Aust. Mus. Reg. No. 221–35).

*Description*

*Front.*—Four-lobed with broad inner and very small outer lobes. The inner lobes are clearly separated by a deep notch and are about 9 times the breadth of the laterals. The inner orbital lobes are about two-thirds the width of the frontal lobes and are *concave.*

*Anterolateral teeth.*—Five, of which the fourth is very small. The remainder decrease in size progressively from front to rear.

*Carapace.*—Hirsute with underneath microscopic granules generally distributed. The following carapace ridges are present: short frontals, mesogastrics, epibranchials, mesobranchials (one pair), and a cardiac. The epibranchial is broadly interrupted at the cervical groove.

*Basal antennal joint.*—Relatively short (length twice breadth) with conspicuous beaded granules and bearing a short crest of enlarged granules.

*Chelipeds.*—Short, robust, the left more massive than the right, and bearing carinae consisting of conspicuous beaded granules. The anterior border of the arm forms a sharp carina which is coarsely granular distally, and bears 4 sharp spines proximally. Wrist bearing 3 or 4 spines on the upper surface in addition to numerous spiniform granules. The 3 usual carinae each ending in a spine are also present. The hands bear conspicuous carinae, 2 on the upper surface and 3 on the outer surface but only a single faint one is present on the inner surface. The inner carina of the upper surface is represented by 3 spines decreasing in size distally, while the outer one is represented by 2 spines of equal size. The 3 carinae of the outer surface are all granular with coarse granules in the uppermost, relatively coarse granules in the middle, and fine granules in the lowermost. Under surface of the hand bearing microscopic granules with a tendency to a squamiform arrangement. Fingers short, stout, and conspicuously carinated.

*Fifth leg.*—Merus moderately long (twice as long as broad) with usual postero-distal spine; posterior border of propodus bearing hairs and spines, 7 subequal spines being visible on the single appendage available. The dactylus bears a terminal point and has numerous small spines on its anterior surface.

*First male pleopod.*—Smoothly curved and regularly tapering to a flared, slightly recurved tip. On the inner surface the basal lobes bear scattered elongate

bipinnate hairs. On the outer surface just beyond the basal lobes there is an occasional short hair, otherwise it is bare up to the terminal armature. On the inner surface beyond the basal lobes there are a few microscopic spinules which form a distantly spaced row, following which there is a bare area, and finally a few sparsely scattered spinules towards the tip. The terminal armature on the outer surface consists of 3 long stout bristles at right angles to the appendage and decreasing in size distally.

*Comments*

Since the discovery of this specimen attempts to obtain others by proxy collections have been made, but have failed. More specimens are required to decide whether Edmondson's *T. medipacifica* is a synonym, as appears probable. There are certainly resemblances between Edmondson's figures of the pleopod (Edmondson 1954, fig. 34*g,h*) and the present specimen. He shows, for example, the microscopic subterminal spinules of the inner surface and stout bristles at right angles to the appendage on the outer surface. The differences are (1) five such bristles instead of three, and (2) two terminal bristles on the inner surface which have no counterpart on the present specimen.

The structure of the male pleopods clearly puts this species in the "*chaptali* group", but in general facies the species is closer to the "*admete* group" (see Stephenson and Hudson 1957, p. 362).

### Thalamita granosimana Borradaile

Figs. 2*E*, 4*A*; Plate 3, Fig. 4; Plates 4*J*, 5*G*

*Thalamita granosimana* Borradaile, 1902, pp. 202–3. Rathbun, 1911, p. 208.
?*Thalamita auauensis* Rathbun, 1906, p. 874, pl. xii, fig. 1. Edmondson, 1951, p. 222; 1954, pp. 257–8, figs. 32*a–d*.
*Thalamita margaritimana* Rathbun, 1911, p. 208, pl. 15, fig. 12.

*Material Examined*

WESTERN AUSTRALIA: ♂ (15 mm), 2 ♀♀ (14 and 21 mm) near bar of South Passage Shark Bay, R. W. George, 14.v.1960, dredged 6 fm sand and weed (W. Aust. Mus. Reg. Nos. 42–60, 32–60, and 43–60 respectively); ♂ (11 mm) near bar of South Passage Shark Bay, R. W. George, 14.v.1960, dredged 6 fm sand and silt (W. Aust. Mus. Reg. No. 37–60); 2 ♀♀ (12 and 22 mm) Maud Landing, R. D. Royce, 20.v.1960, dredged 10 fm weed, sand, rock (W. Aust. Mus. Reg. Nos. 109–60 and 106–60 respectively).

*Material illustrated.*—First-mentioned specimen (No. 42–60) above.

*Description*

*Front.*—Two broad lobes, separated by a distinct notch, with a square-cut or slightly concave profile. Inner orbital lobes broad (*c.* 7/10 width of frontal lobes) and not arched.

*Anterolateral teeth.*—Five, the first the largest, the second, third, and fifth sharp and subequal, and the fourth much the smallest. In one specimen the fourth teeth are almost rudimentary.

*Carapace.*—All the normal ridges are present and obvious, with the epibranchials interrupted by the cervical groove but not medianly and with only a single pair of

mesobranchials. Apart from the ridges, the entire surface is hirsute, the hairs covering minute granulations.

*Basal antennal joint.*—Bearing an acute ridge of 8–12 fused tubercles. Ratio between breadth of joint and major diameter of orbit 1·2–1·3.

*Chelipeds.*—Short and stout, left larger than right (in the 2 intact specimens). Upper and outer surfaces coarsely granular, inner and lower surfaces either smooth or bearing faint squamiform granulations. Arm and wrist normal. Upper surface of hand with the 4 usual spines excluding that at the wrist articulation, the anterior outer one being reduced to a tubercle. Outer surface of hand bearing 3 prominent carinae composed of rounded tubercles with granular areas between the carinae. Space between 2 lowermost carinae of outer surface typically finely granular, occasionally smooth. Inner surface of hand without distinct carinae but in some cases with a short row of rounded tubercles. Fingers short and stumpy.

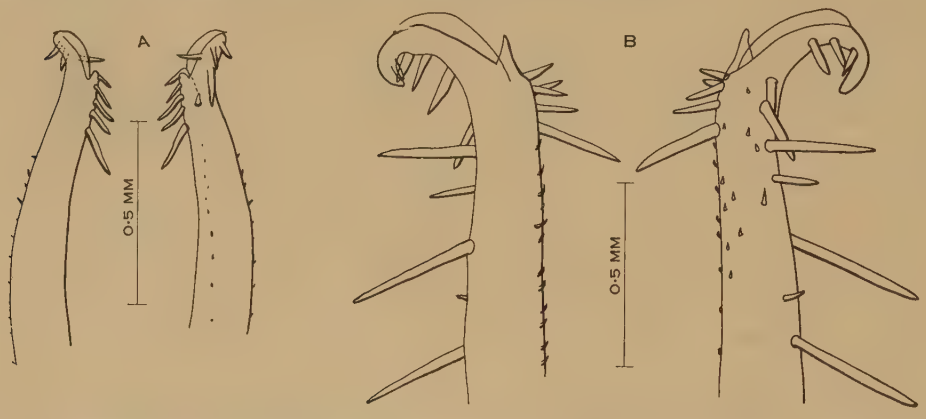


Fig. 4.—Tips of left first male pleopods. Upper surfaces to the left of the scale lines; under surfaces to the right. *A, Thalamita granosimana; B, T. parvidens.*

*Fifth leg.*—Merus moderately long, $2\frac{1}{4}$–$2\frac{1}{2}$ times as long as broad, and smooth posteriorly except for the usual spine. Posterior border of propodus bearing 6–9 spines.

*First male pleopod* (based on two specimens).—Relatively stout, curving smoothly and evenly to a spoon-shaped tip. The inner surface bears proximally a narrow flange with regularly arranged bipinnate hairs, following which it is bare until beyond the middle. Thereafter there is a sparse series of short, forwardly directed spines which merge into the subterminal armature. Outer surface bare to the terminal armature. Terminal bristles on the inner side—2 or 3 short stout backwardly directed spines on the spooned area followed at some distance by about 4 short outwardly or forwardly directed spines; the spinous row then merges with the forwardly directed spines mentioned above. Terminal bristles on the outer side: 1 stout spine on the spooned area followed by 5 stout backwardly directed spines whose size increases distally. The under surface bears a single, short, stout, forwardly directed spine near the tip, followed proximally by a single row of very small forwardly directed hairs.

*Comments*

In general structure, this species belongs to the *admete* group, but in its pleopod structure, it belongs to the *chaptali* group. It is obviously somewhat distant from *T. admete* although originally described as a variety of it.

The original description of *T. granosimana* is too abbreviated to permit certain identification of the present specimens, but the only possible discrepancy concerns the under surface of the hands. In Borradaile's description these are given as "granular" and also "granular as in *T. sima*". At first sight the under surfaces of the chelipeds of the present specimens appear quite smooth but in fact they carry a faint squamiform pattern resembling, but far less obvious than, that in *T. sima*.

*T. margaritimana* Rathbun, 1911, is probably a synonym of *T. granosimana*, the only difference in the descriptions being that it has a vestigial fourth anterolateral tooth. However, Rathbun's figure (pl. 15, fig. 12) suggests the presence of a more than vestigial tooth at least on the right side of her specimen. In view of the considerable variation in the size of the fourth tooth in *T. admete* it seems unwise to separate *T. margaritimana* from *T. granosimana* solely on the basis of this feature.

Similar variation apparently occurs in *T. auauensis* Rathbun, 1906, (see Edmondson 1954, p. 257) and once again no features of the general facies appear to separate the two species. The position as regards the first male pleopod is somewhat uncertain. In general form it closely resembles that of the present species (see Edmondson 1954, fig. 32*c*), but the form of the tip may be different. Thus Edmondson figures four large bristles on either side as against three and five respectively on typical representatives of the present series.

### Thalamita inhacae Barnard

*Thalamita inhacae* Barnard. Stephenson and Hudson, 1957, pp. 337–9, figs. 2*L*, 3*L*, pl. 3, fig. 2, pls. 7*H*, 10*E*.

*Material Examined*

WESTERN AUSTRALIA: ♀ 16 mm, Yampi Sound, intertidal, G. A. Robinson, Nov. 1959 (W. Aust. Mus. Reg. No. 16–60).

New record for Western Australia.

### Thalamita integra Dana

*Thalamita integra* Dana. Stephenson and Hudson, 1957, pp. 339–41, figs. 2*H*, 3*H*, pl. 3, fig. 3, pls. 7*I*, 10*F*.

*Material Examined*

WESTERN AUSTRALIA: 6 ♂♂ (14–20 mm), 2 ♀♀ (17, 25 mm), Pidgeon I. Wallabi Group, Abrolhos Is., P. Barrett Lennard, May 1959 (W. Aust. Mus. Reg. No. 1–60); ♂ (24 mm) E. Wallabi I., Abrolhos Is., T. Richert, 12.v.1960, hand-collected in 8 ft of water (W. Aust. Mus. Reg. No. 45–60); ♂ (32 mm) Pidgeon I. Wallabi Group, Abrolhos Is., P. Barrett Lennard, May 1959, intertidal, sand and rock bottom (W. Aust. Mus. Reg. No. 110–60).

New record for Western Australia.

### Thalamita intermedia Miers

*Thalamita intermedia* Miers, 1886, p. 196, pl. xvi, fig. 1. Stephenson and Hudson, 1957, pp. 341–3, fig. 4, pl. 3, fig. 4, pl. 10*G*.

Recent Western Australian collections comprise 10 specimens from the following localities:—W. approaches to Mermaid Strait; NE. of Malus I., Dampier Arch.; W. of Flat I. near Long I. off Onslow; between Malus and Gidley Is.; 3–4 miles off Delambre I., Dampier Arch.; Exmouth Gulf, W. side; and Legendre I., Dampier Arch.

The collection contained a single male (23 mm, W. approaches to Mermaid Strait, R. D. Royce, 27.v.1960, dredged 20 fm coral and sand, W. Aust. Mus. Reg. No. 107–60), which is abnormal in possessing three frontal lobes on the left side. The normal lateral lobe is divided by a distinct notch into a submedian lobe and a lateral, the ratio of whose widths are approximately 1 : 2.

### Thalamita macropus Montgomery

*Thalamita macropus* Montgomery. Stephenson and Hudson, 1957, pp. 343–4, figs. 2*J*, 3*J*, pl. 4, fig. 1, pls. 7*J*, 10*H*.

*Material Examined*

WESTERN AUSTRALIA: 2 ♂♂ (10, 14 mm), 2 ♀♀ (10 mm, 17 mm), 4 miles W. of Cape St. Cricq, Dorre I., Shark Bay, R. W. George, 16.v.1960, dredged 40 fm (W. Aust. Mus. Reg. No. 47(*b*)–60).

This species is known only from Western Australia and New South Wales, with the Abrolhos Is. as the type locality.

### Thalamita parvidens (Rathbun)

Figs. 2*F*, 4*B*; Plate 4, Fig. 1; Plates 4*K*, 5*H*

*Thalamonyx parvidens* Rathbun, 1907, p. 62, pl. 5, fig. 9.
*Thalamita parvidens* (Rathbun). Sakai, 1939, pp. 425–6, fig. 19.

*Material Examined*

WESTERN AUSTRALIA: ♂ (27 mm) near bar of South Passage Shark Bay, R. W. George, 14.v.1960, dredged 6 fm sand and silt (W. Aust. Mus. Reg. No. 35–60); ♂ (20 mm) ♀ (22 mm) data as above (W. Aust. Mus. Reg. No. 39–60); ♀ (17 mm) (ovigerous) data as above (W. Aust. Mus. Reg. No. 40–60); 7 ♂♂ (10–36 mm), ♂ (31 mm, stalked barnacles on carapace), ♀ (15 mm), 4 ♀♀ (ovigerous) (24–29 mm) Maud Landing, R. D. Royce, 21.v.1960, dredged sand and weed 7 fm (W. Aust. Mus. Reg. No. 61–60); ♂ (19 mm) W. of Flat I. near Onslow, B. R. Wilson, 19.v.1960, dredged 6–10 fm (W. Aust. Mus. Reg. No. 64–60).

*Material illustrated.*—First-mentioned specimen above.

*Description*

*Front.*—Two broad lobes, separated by a distinct notch. Inner orbital lobes slightly arched and about half the breadth of the frontal lobes. Ventral inner orbital lobes rounded and reasonably prominent.

*Anterolateral teeth.*—Relatively square-cut in larger and relatively sharp in smaller specimens. Five teeth, the first four stout and relatively blunt (at least in

larger specimens). The fourth is about half the size of the third, and the fifth is the sharpest and most protruding.

*Carapace.*—Breadth about 1½ times length. Bearing short sparsely arranged hairs underlaid by small granules. All the normal carapace ridges are present (see Stephenson and Hudson 1957, fig. 1). The mesogastrics are broadly interrupted in the mid-line, and the cardiac is represented by two very small broadly separated indistinct ridges. The frontals consist of a rounded cluster of granules and the single pair of mesobranchials are markedly prominent.

*Basal antennal joint.*—Approximately the diameter of the orbit and bearing an elevated crest surmounted by rounded granules.

*Chelipeds.*—The right larger than the left, particularly in males, all bearing stout sharp spines. The upper surfaces hairy and bearing small granules which tend to form a squamiform pattern; the lower surface typically smooth and polished, but occasionally bearing traces of squamiform markings. Anterior border of the arm bearing either 3 or 4 spines. Outer surface of the wrist with 3 spines, the uppermost and lowermost marking the ends of distinct carinae. The spine on the inner surface of the wrist is rather long, about one-quarter the length of the palm. Upper surface of the hand with 2 inner spines and 2 outer spines or tubercles, apart from that at the wrist articulation. Outer surface with 3 carinae. The lowermost, which continues along the immovable finger, is sharp, smooth, and distinct. The middle one, also distinct, is sometimes smooth and sometimes partially resolvable into a number of large rounded granules. The uppermost consists of a row of granules, sometimes complete and sometimes barely recognizable. Between these carinae there are traces of squamiform markings. Inner surface of hand with no trace of a carina, typically smooth and polished but sometimes bearing traces of squamiform markings. Fingers relatively short, stout, sharp, and deeply grooved.

*Fifth leg.*—Merus relatively short, length twice breadth (2½ times according to Rathbun (1907)) and smooth posteriorly, except for a large stout spine. Posterior border of propodus bearing 4–6 spines.

*First male pleopod* (based on 11 specimens).—Relatively stout, curving smoothly and evenly to the slightly flared, strongly recurved tip. The inner surface bears proximally a cluster of fine bipinnate hairs followed by a slightly flared area which sometimes bears similar hairs. Thereafter it is either bare or carries a sparse series of short, forwardly directed spines. Outer surface bare in the proximal half then either bare or carrying a sparsely arranged row of short, curved, forwardly directed spines. When present these become commoner just behind the terminal armature. Terminal bristles on the inner side large and stout. Normally there is a distal and a proximal series. The distal series which corresponds in position roughly with the recurved part of the appendage consists of 3–9 stout recurved bristles. The proximal series consists of 2 or 3 very long stout bristles which are slightly recurved, with between them 1–4 shorter and thinner bristles. Terminal bristles on the outer side, 3–5 stout bristles increasing in size proximally. The under surface usually bears subterminally a scattered series of short, fine, forwardly directed spines.

Sakai's (1939) figure does not show any of the most distal bristles on the inner side.

*Colour.*—After 2 months in alcohol, with complicated mottling in red-orange and reddish brown.

*Comments*

The species resembles *T. chaptali* in general facies and also in the general form of the male pleopod with its recurved tip. It differs in the more distinct frontal notch; in the mesogastric ridge being broadly interrupted at the mid-line; in the more distinct spines on the upper surface of the cheliped; in the shape of the penultimate segment of the male abdomen; and in the details of the terminal bristles of the male pleopod.

The male pleopod shows resemblances to *T. poissoni* but differs in the details of terminal armature.

Sakai's (1939) description says "the carapace has no transverse ridges on cardiac and post-branchial regions", but his illustration (text fig. 19*a*) shows a pair of mesobranchial ridges as does Rathbun's original plate (Rathbun, 1907, pl. 5, fig. 9). In the present specimens the "rudiments" of cardiac ridges are also distinguishable.

This species was incorrectly placed in the key previously published (Stephenson and Hudson 1957, p. 318) in that the median frontal notch is distinct. It keys out with *T. sima* H. Milne Edwards and *T. iranica* Stephensen. It differs from the former in having rounded granules on the crest of the basal antennal joint. The broadness of the anterolateral teeth varies with the size of the specimen and does not form an effective basis for separation from *T. iranica*, which the species resembles in general facies. Separation is easily effected by the form of the male abdomen and pleopods.

## Thalamita trilineata Stephenson & Hudson

Plate 4, Figs. 2, *L*

*Thalamita trilineata* Stephenson and Hudson, 1957, pp. 359–60, figs. 2*E*, 3*E*, pl. 6, fig. 4, pls. 8*S*, 10*L*.

*Material Examined*

WESTERN AUSTRALIA: ♂ (22 mm) ♀ (10 mm) Maud Landing, 20.v.1960, R. D. Royce, dredged 10 fm sand, weed, rock (W. Aust. Mus. Reg. No. 84–60).

*Comments*

This species which was only known from the Queensland holotype is easily recognizable by the carapace ridges and the form of the male pleopod.

Alterations and amplifications of the original description are: (1) median frontal notch narrow but deep, (2) inner orbital lobes "arched" rather than "slightly arched", (3) 5 anterolateral teeth, the fourth conspicuously the smallest, (4) mesogastric carapace ridge with an inconspicuous median interruption, (5) posterior border of propodus of fifth leg bearing 5–8 spines.

In the present specimens the front is clearly four-lobed.

This species was unfortunately omitted from the previous key (Stephenson and Hudson 1957, p. 316) but its relationship to that key was clearly given in the comments on the species (see Stephenson and Hudson 1957, p. 360).

## III. Discussion

Following the four earlier papers of the present series (Stephenson and Hudson 1957; Stephenson, Hudson, and Campbell 1957; Stephenson and Campbell 1959; Stephenson and Campbell 1960) it was hoped that the study of the detailed taxonomy and distribution of the Australian portunids was sufficiently complete for about a decade to elapse before further publications would become desirable. Hence a paper (Stephenson 1961) reviewing the biogeography and evolution of the Australian portunids was presented at the Centenary Meeting of the Royal Society of Victoria (December 1960) and is in the press.

Almost immediately afterwards rich collections were obtained by dredging off the coast of Western Australia, and this material contributes predominantly to the present paper. It is evident that future additions to the Australian portunid fauna can be expected, not only by intertidal collecting in northern and north-western Australia, but also by dredgings from the entire northern half of the continent.

Because new species are described in the present paper, revisions of the previously published keys should be undertaken. This is also necessary because of past omissions from the keys; for example *Portunus rugosus* (A. Milne Edwards, 1861), *P. euglyphus* (Laurie, 1906), *Thalamita squamosa* Stephenson & Hudson, 1957, *T. trilineata* Stephenson & Hudson, 1957, and *Lupocyclus tugelae* Barnard, 1950. These revisions are deferred because several undescribed species are known to be present in the collections of the Muséum National d'Histoire Naturelle, Paris, and these are likely to be described shortly.

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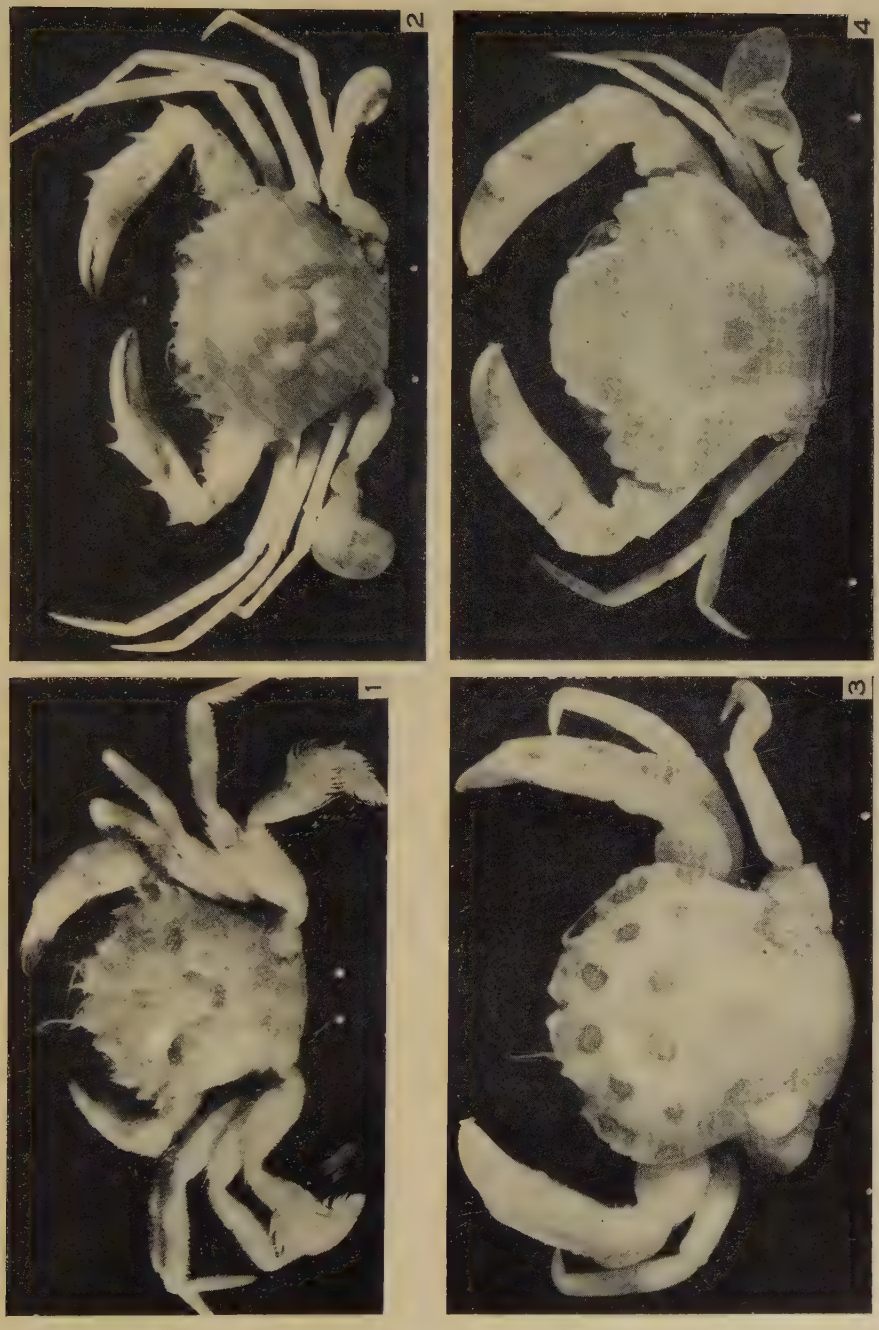
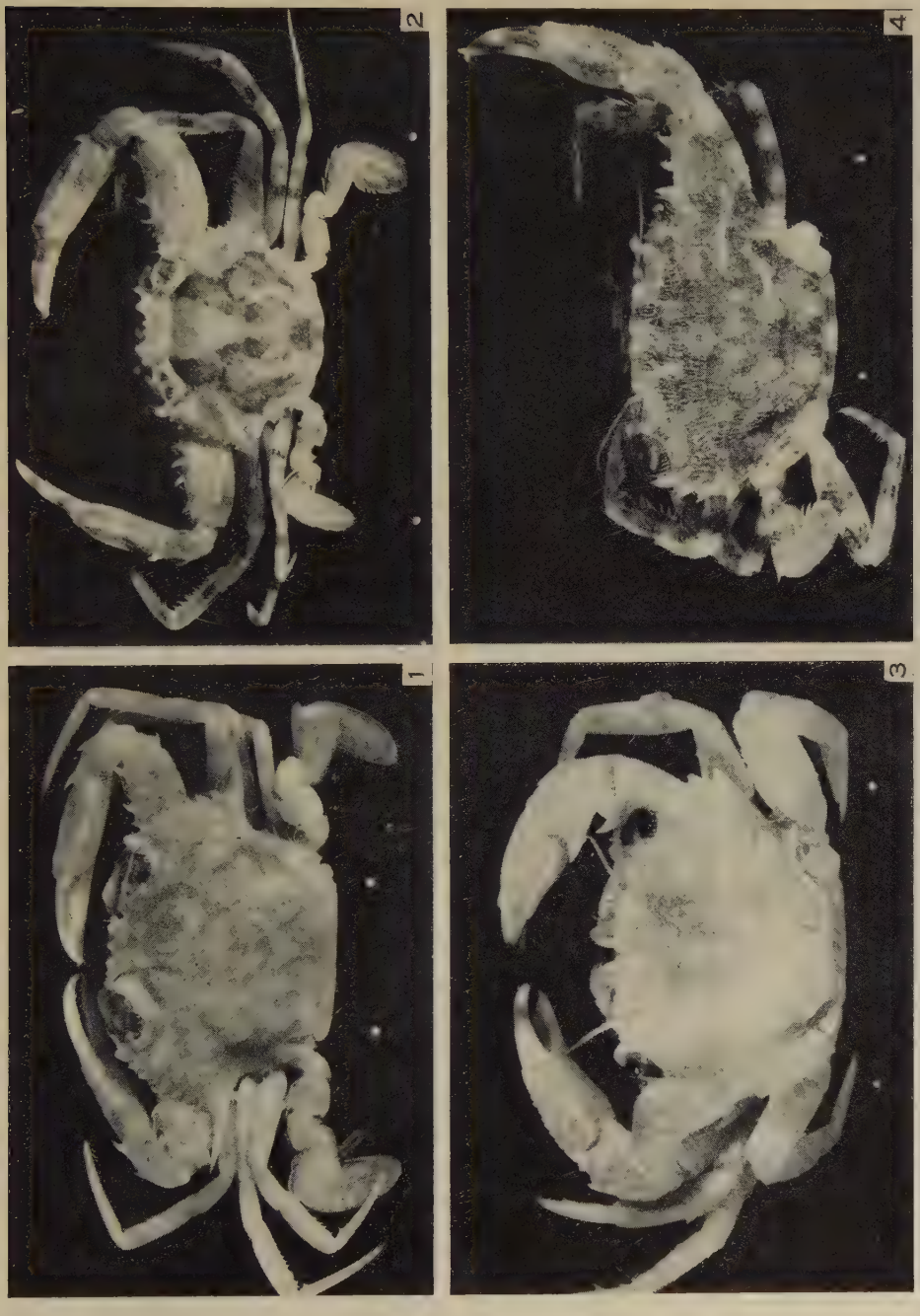
AUSTRALIAN PORTUNIDS. V



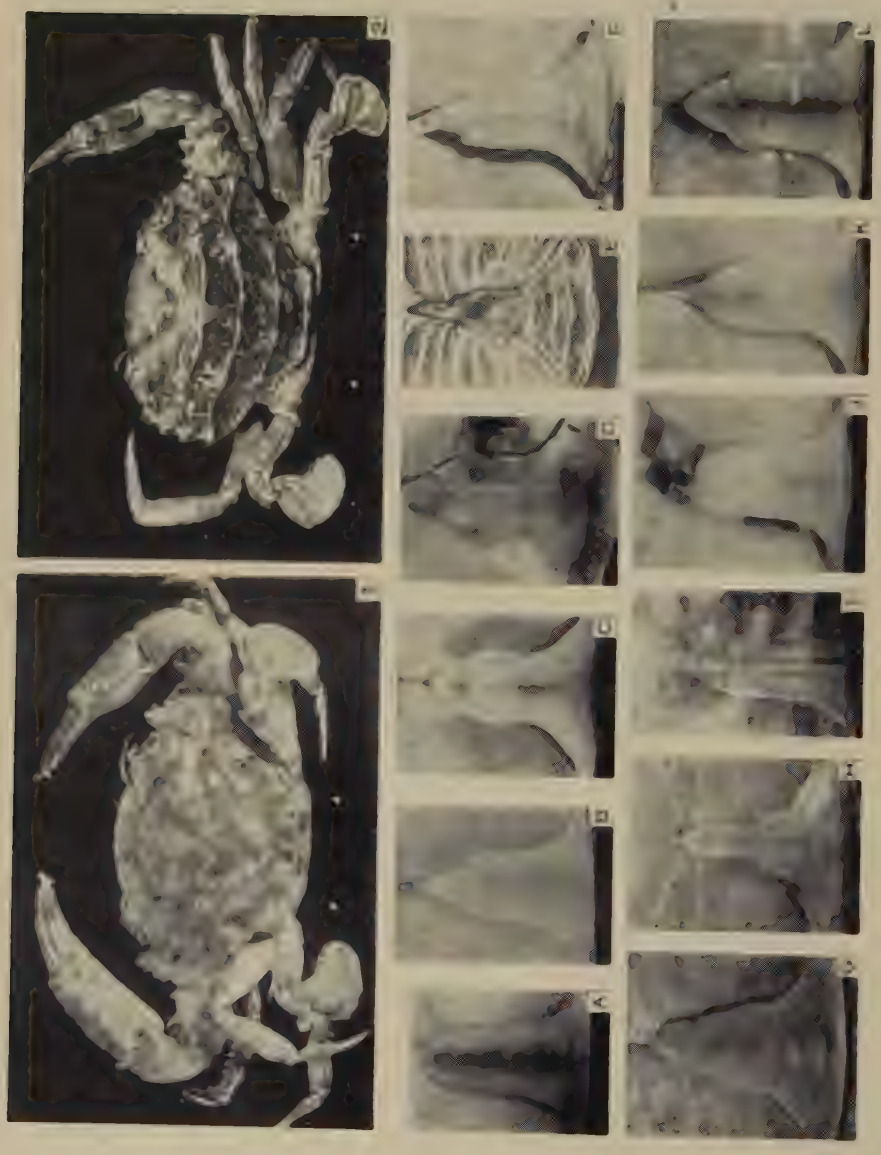

Distance between sealing white dots 1 cm. Fig. 1. *Vectocarcinus spinifrons*. Fig. 2.—*Parathranites orientalis*. Fig. 3.— *Caphyra yookalai*. Fig. 4. *Lissocarcinus laevis*.

Distance between scaling white dots 1 cm. Fig. 1.—*Lupocyclus tugelae*. Fig. 2.—*Portunus argentatus*. Fig. 3.—*P. curvipenis*. Fig. 4.—*P. pseudoargentatus*.

AUSTRALIAN PORTUNIDS. V

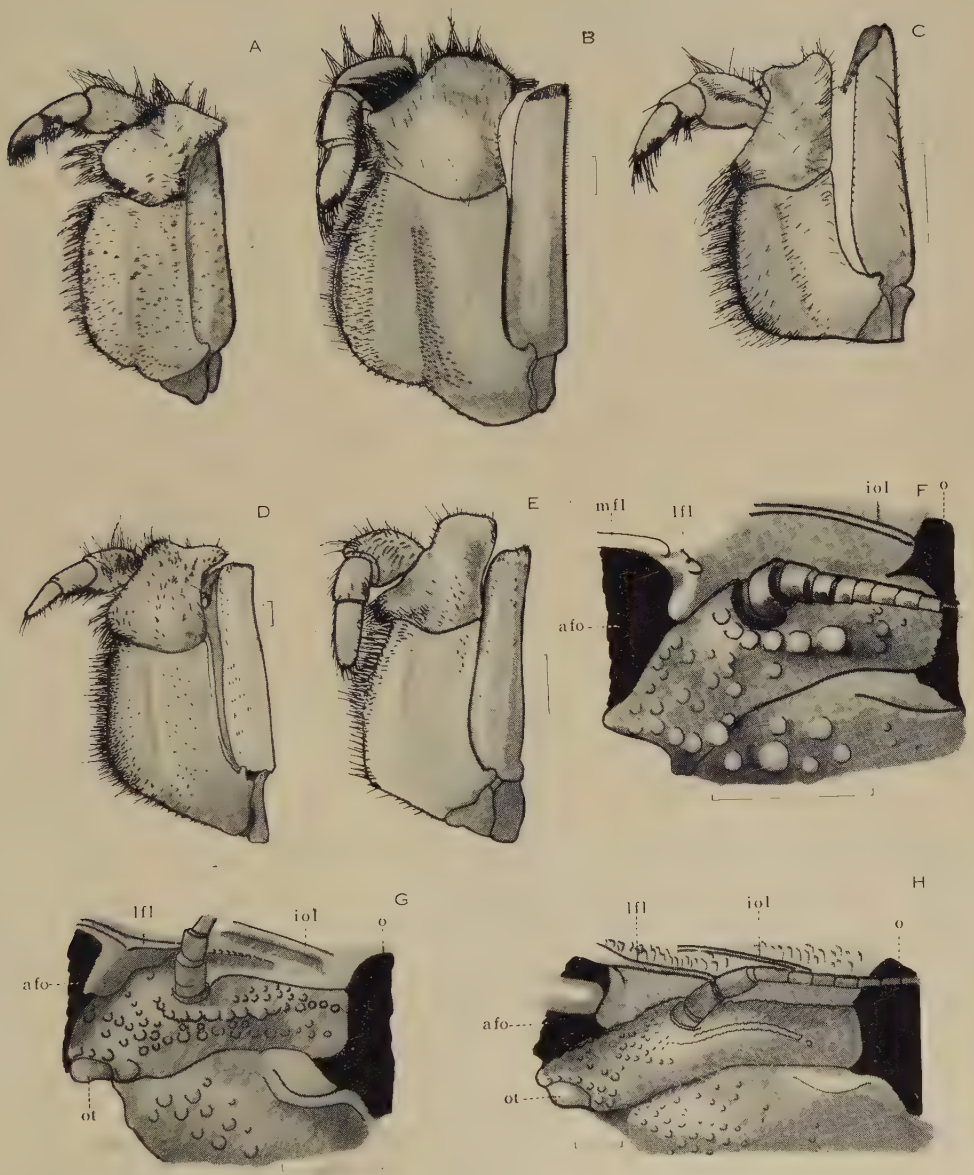



Distance between scaling white dots 1 cm. Fig. 1.—*Portunus rugosus*. Fig. 2.—*P. temicaudatus*. Fig. 3.—*Thalamita dakini*. Fig. 4. *T. granosimana*.



Distance between scaling white dots 1 cm. Fig. 1.—*Thalamita parvidens*; Fig. 2.—*T. trilineata*; Figs. *A–L*.—Male abdomens. *A*, *Nectocarcinus antipodum*; *B*, *Portunus pelagicus*; *C*, *Lissocarcinus laevis*; *D*, *Portunus argentatus*; *E*, *P. curvipenis*; *F*, *P. pseudoargentatus*; *G*, *P. rubromarginatus*; *H*, *P. haanii*; *I*, *Thalamita admete*; *J*, *T. gracilipes*; *K*, *T. parvidens*; *L*, *T. trilineata*

AUSTRALIAN PORTUNIDS. V




Wash drawings of left third maxillipeds of species of *Portunus* (Figs. *A*–*E*) and left basal antennal joints of species of *Thalamita* (Figs. *F*–*H*). Scale lines 1 mm. *A*, *Portunus argentatus*; *B*, *P. curvipenis*; *C*, *P. tenuicaudatus*; *D*, *P. pseudoargentatus*; *E*, *P. rugosus*; *F*, *Thalamita dakini*; *G*, *T granosimana*; *H*, *T. parvidens*; *afo*, fossa of first antenna; *iol*, inner orbital lobe; *mfl*, median frontal lobe; *lfl*, lateral frontal lobe; *o*, orbit; *ot*, otolith.

# HYDROLOGY OF THE INDIAN OCEAN

## I. THE WATER MASSES IN INTERMEDIATE DEPTHS OF THE SOUTH-EAST INDIAN OCEAN

By D. J. Rochford*

[*Manuscript received July* 6, 1961]

*Summary*

Three water masses have been identified from maxima and minima in temperature–salinity diagrams for intermediate depths of the south-east Indian Ocean.

(1) The Antarctic Intermediate occurred as a salinity minimum within the density range of 27·00–27·28 $\sigma_t$.

(2) The North-West Indian Intermediate was found as a salinity maximum within the $\sigma_t$ range 27·20–27·50.

(3) The Banda Intermediate, lying below the North-West Indian Intermediate, had the characteristic of a salinity minimum within the $\sigma_t$ range of 27·28–27·59.

Preformed phosphate has been found useful as a third conservative property for the identification of major paths of spreading. The distribution and paths of spreading of the three water masses are shown in charts of the Indian Ocean east of 90° E.

### I. Introduction

Hydrological data collected east of 90° E. in the Indian Ocean before 1958 were few in number and very irregularly spaced in time and location. They were used (Rochford 1958) to examine the circulation on the 27·20 $\sigma_t$ surface, but only the very broad features of the water masses involved, and their circulation, could be determined.

Using data from similar sources, Wyrtki (1961*b*), in his study of the physical oceanography of south-east Asian waters, examined the various core layers of the northern Indian Ocean east of 90° E. More recently Tchernia and Lizeray (1960) examined the hydrological structure and circulation along a section, worked during the early autumn of 1958, from north-west Australia to the Sunda Strait. These authors suggested that Pacific water moves through the Banda Sea into the Indian Ocean.

Six cruises have been made by H.M.A.S. *Diamantina* since the end of 1959 to explore in detail the hydrological structure of the eastern Indian Ocean. The exploratory phase has been completed and in this paper, the first of a series discussing the results, consideration is given to the intermediate depth circulation.

### II. Materials and Methods

The data used in this paper are published in C.S.I.R.O. Aust. (1961*a*, 1961*b*, 1961*c*, 1961*d*). All phosphate data have been corrected for salt error by multiplying the results by 1·1. The depth of the core layer (Wüst 1935) and the values of the

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identifying properties used have, in most cases, been determined from smoothed vertical profiles.

Figure 1 shows the positions of the stations used.

## III. Salinity–Temperature Relations of Intermediate Depth Waters

A symmetrical $T$–$S$ curve around the intermediate salinity minimum of Antarctic origin was found only towards the southern limit of the region (Station Dm 1/47/60, Fig. 2). Elsewhere the symmetry of this $T$–$S$ relation was distorted

Fig. 1.—Chart showing *Diamantina* stations. ×, Cruise Dm 2/59; ▲, Cruise Dm 1/60; *, Cruise Dm 2/60; ⊙, Cruise Dm 3/60.

by a series of minor maxima and minima of salinity. The maxima were associated with the spreading of a high salinity North-West Indian Intermediate water mass, presumably of Red Sea origin (Wyrtki 1961*a*), and can be readily identified on the $T$–$S$ curve as far south as Station Dm 1/79/60 (Fig. 2) in latitude 22° S. and with less certainty to about 32° S. (see also Section V). The minima were associated with the drift of a low salinity water from the Banda Sea (see Section VI) and could be detected in the $T$–$S$ curves to about 22° S. (Station Dm 2/79/59, Fig. 2).

Throughout its distribution the Antarctic Intermediate water mass possessed a higher temperature at comparable salinities than the other two intermediate water masses (Fig. 3) and therefore had the lowest density range ($\sigma_t$ 27·00–27·28). The North-West Indian Intermediate had a density range of $\sigma_t$ 27·20–27·50 and the Banda of $\sigma_t$ 27·28–27·59. At lower temperatures (*F* and *G* in Fig. 3) the North-West Indian Intermediate and the Banda water masses were strongly influenced by the deep salinity maximum, but the Antarctic Intermediate was not influenced at any stage.

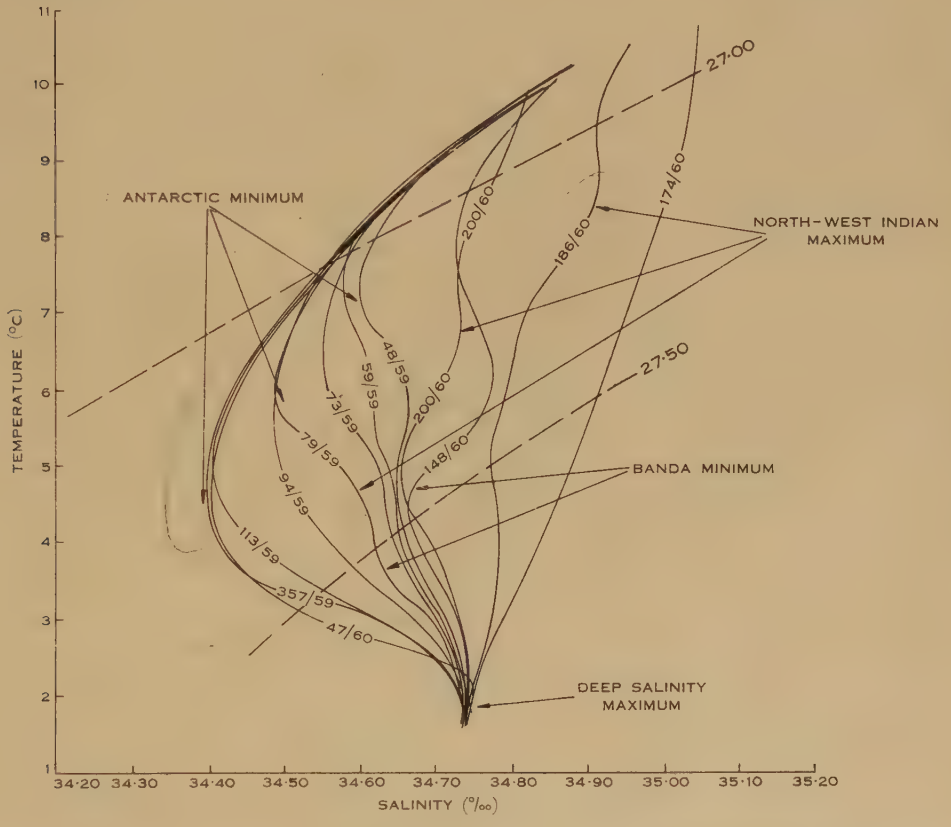


Fig. 2.—Selected *T–S* curves within the temperature and salinity limits of the intermediate circulation of the south-east Indian Ocean.

## IV. Distribution of the Core Layer of the Antarctic Intermediate Water Mass

North of 35° S. this core layer was always deeper to the west of the 105° E. meridian (Fig. 4). Within the whole region north of 35° S. its depth decreased from about 1100 m in the south to 500 m in the north. South of 35° S. only small variations were noted in its depth of occurrence. The lowest salinity (34·38‰) of this layer occurred in the south of the region (Fig. 5); salinity then increased slowly

with distance to the north, as far as 25° S. Northwards from this latitude the zonal gradients of salinity became more pronounced, with the highest salinities (34·70–34·72‰) in the western side only. Wyrtki (1961*a*) from a study of the dynamic topography, considered that the change in meridional salinity gradients at about 25° S. marked the boundary to the south of which actual movements, and to the north of which horizontal mixing within the intermediate depth waters are more pronounced.

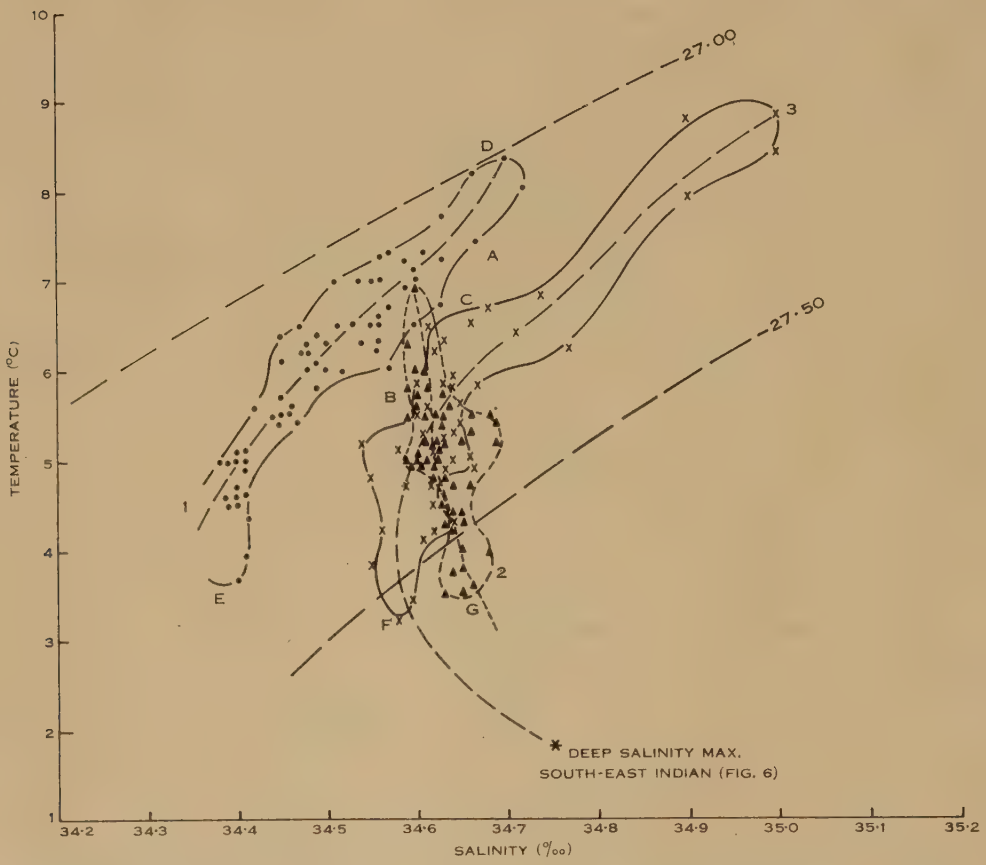


Fig. 3.—The temperature–salinity limits of the water masses of the intermediate circulation. ●, Antarctic Intermediate with entry properties at *1*; ×, North-West Indian Intermediate with entry properties at *3*;, ▲ Banda Intermediate with entry properties at *2*. The isopycnal surfaces, 27·00 and 27·50 $\sigma_t$, have been entered. The letters refer to mixing regions.

Because the zonal gradients in salinity within this layer were small (Fig. 5), it was difficult to determine from salinity data alone the paths of northward spreading of Antarctic waters. Figure 6 shows that a preformed phosphate P (Redfield 1942) value of 0·90 μg-atom/l or more was found only within the Antarctic Intermediate water mass and the deep southern limit of the North-West Indian Intermediate water mass. Within the core layer of the former water mass, waters with

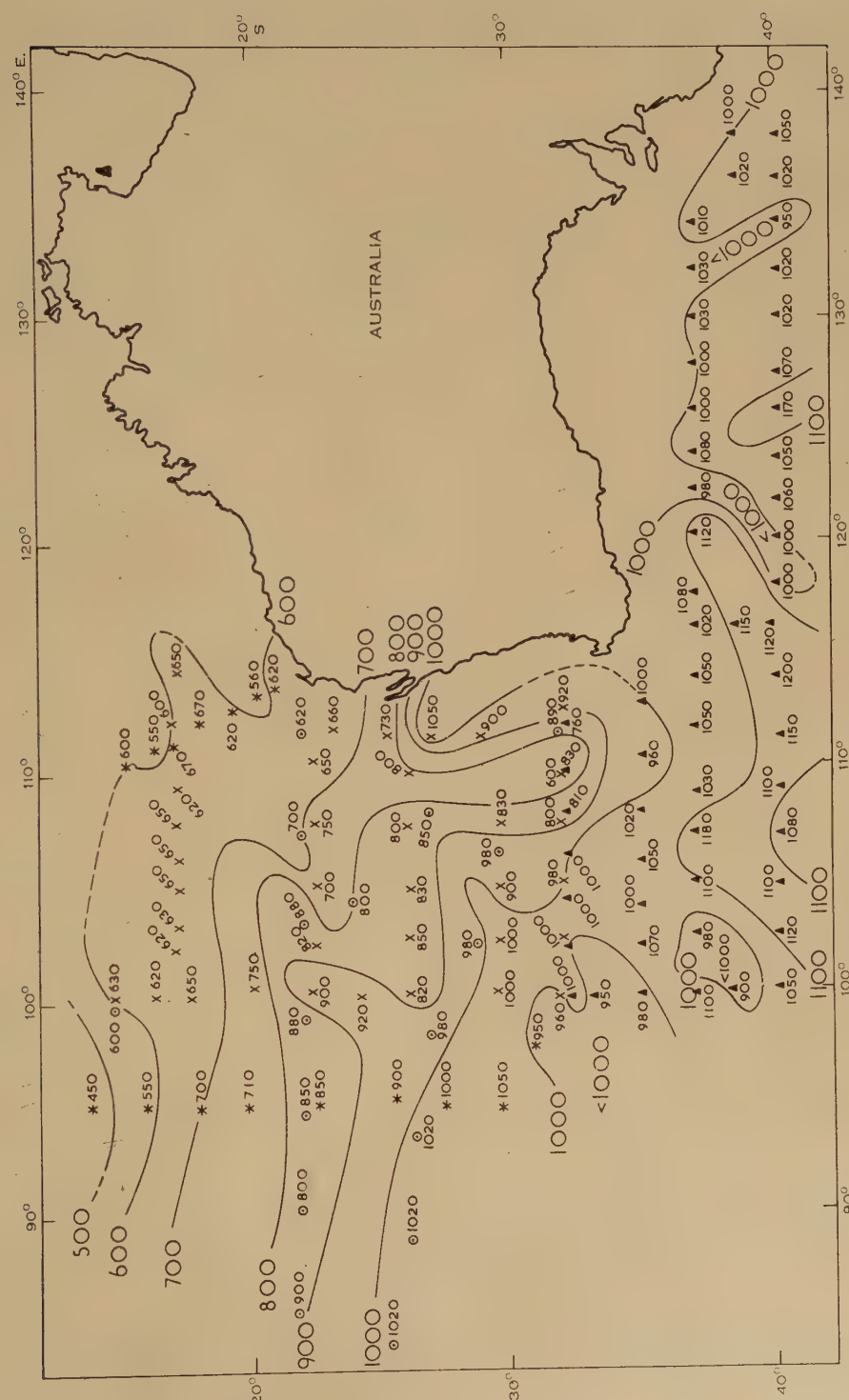


Fig. 4.—The depth (m) of the Antarctic Intermediate water mass.

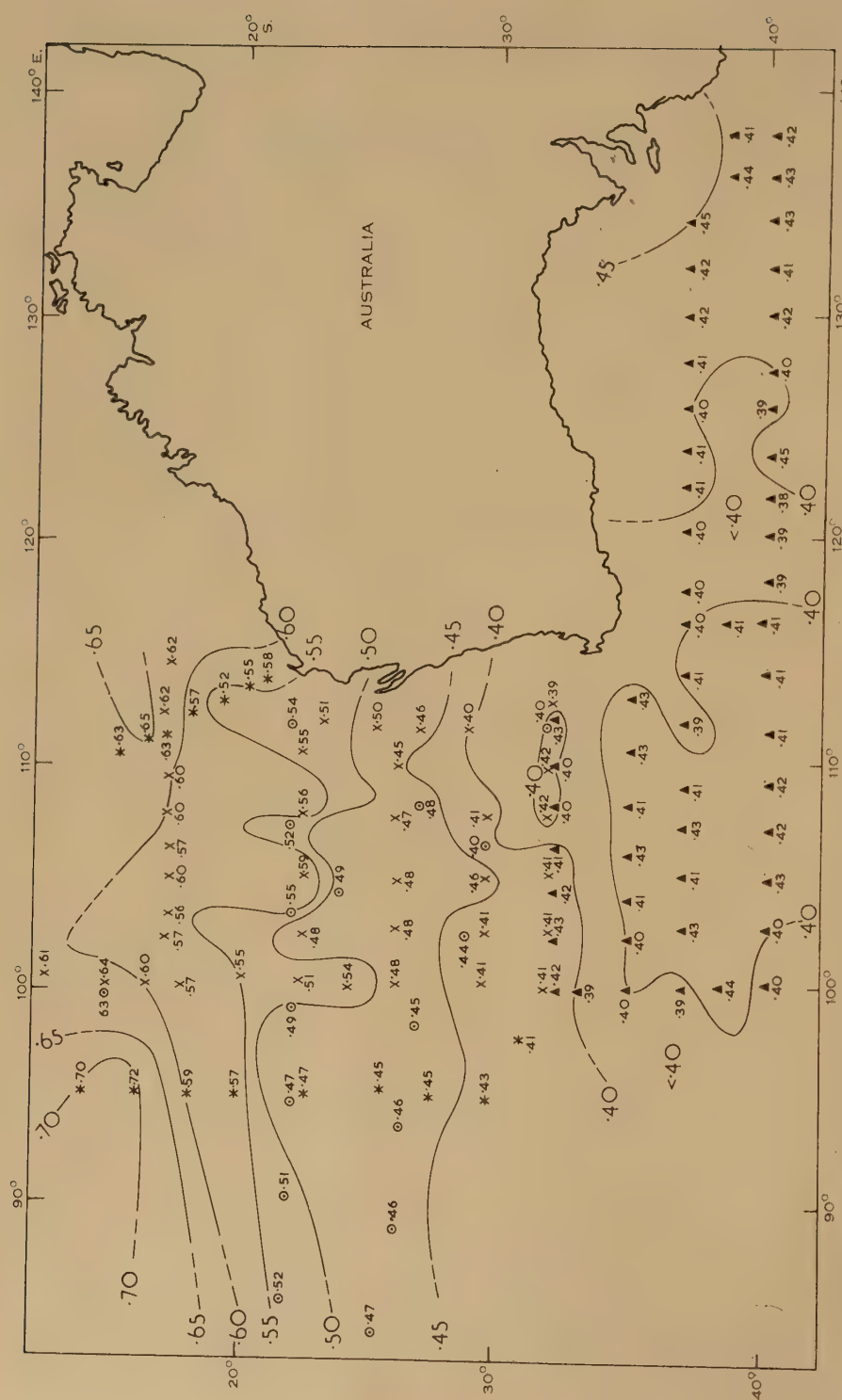


Fig. 5.—The salinity of the Antarctic Intermediate water mass. 34·00 should be added to the values to obtain the actual salinity.

a preformed phosphate P content of 0·90 μg-atom/l or more must be associated principally with horizontal spreading of the Antarctic Intermediate water mass,

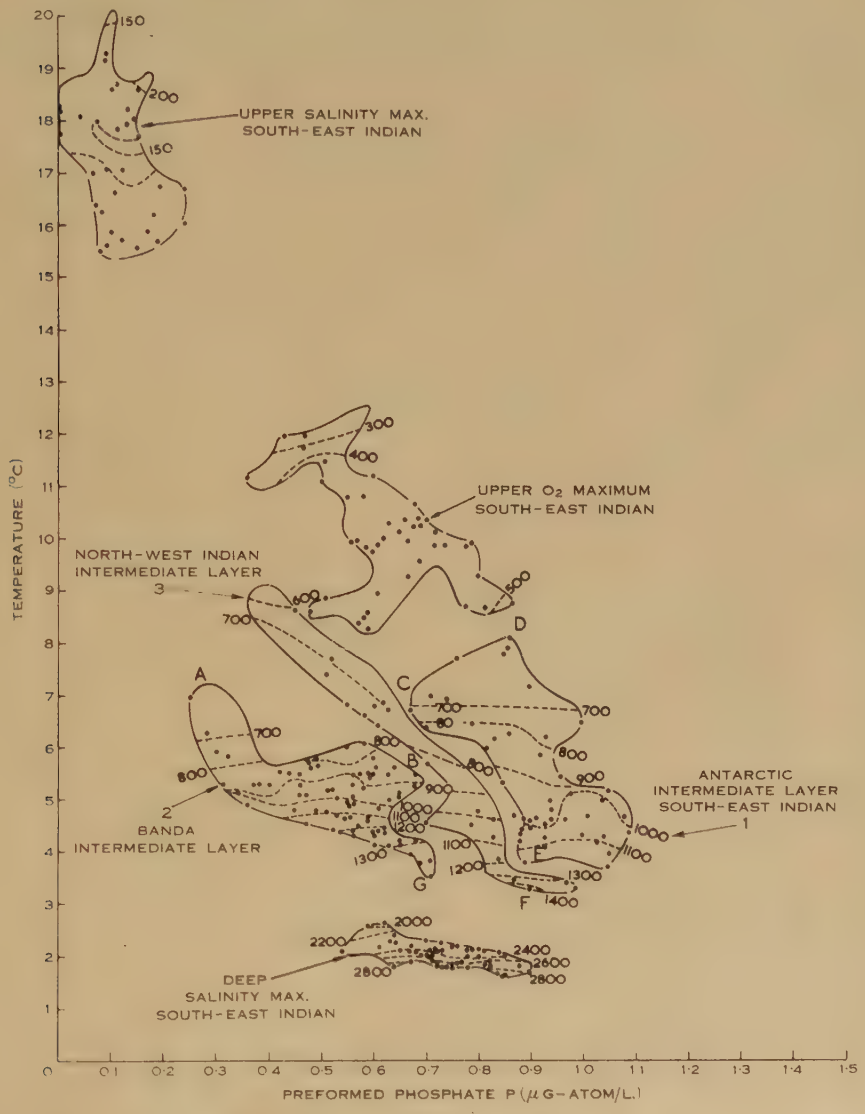


Fig. 6.—The temperature–preformed phosphate limits of the major water masses of the south-east Indian Ocean. Numbers refer to entry properties of the three intermediate water masses (Fig. 3) and letters to the mixing regions of the intermediate circulation (Fig. 3).

and with vertical mixing only to a very limited extent in the southern part of the region. Waters with these high preformed phosphate values were found north of

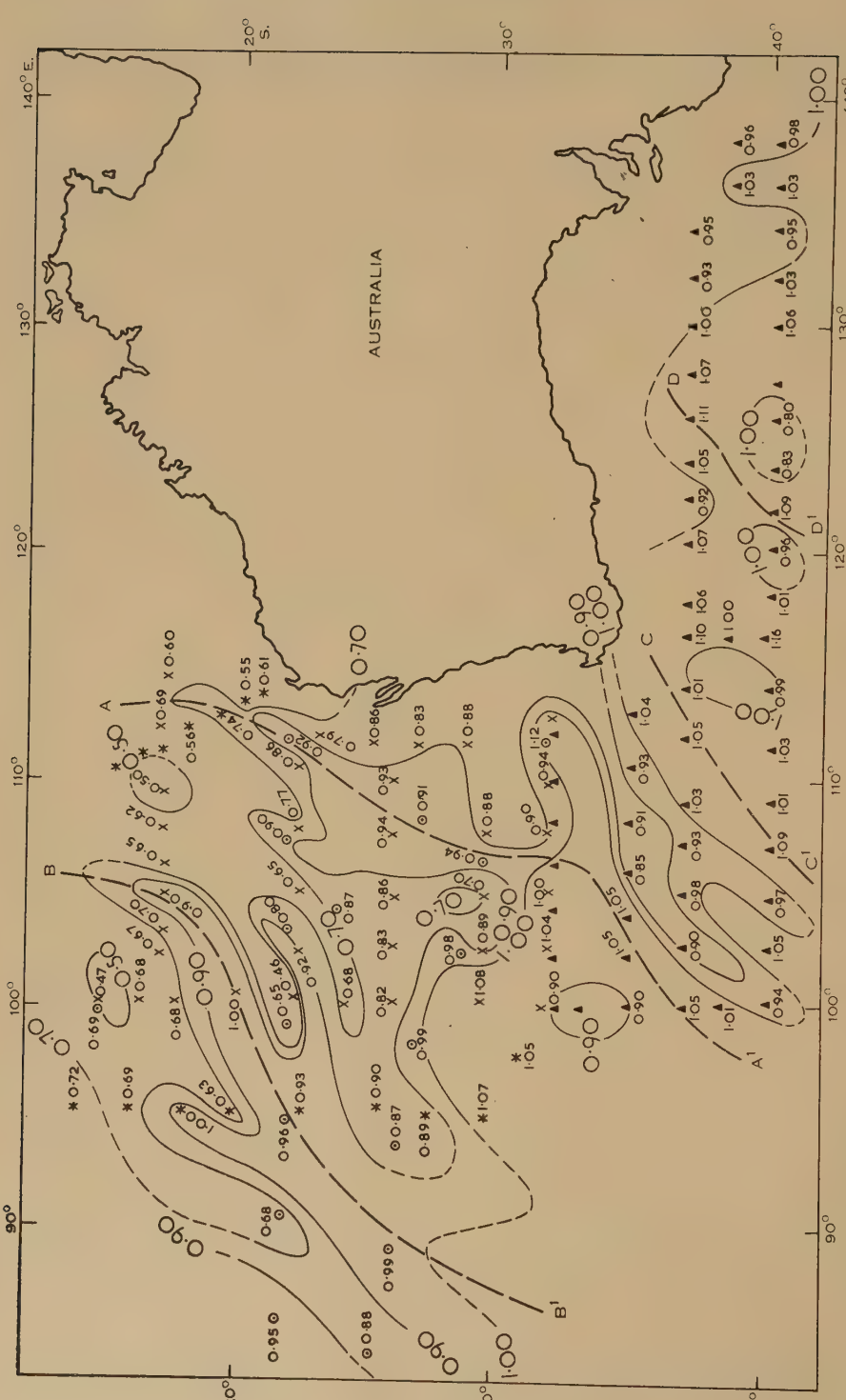


Fig. 7.—The preformed phosphate P(μg-atom/l) of the Antarctic Intermediate water mass. $AA^1$, $BB^1$, $CC^1$, $DD^1$ denote regions of maximum values.

25° S. (*A* and *B* in Fig. 7), and the paths ($AA^1$ and $BB^1$ in Fig. 7) were considered the major routes for the northward spreading of the Antarctic Intermediate water mass. These two paths can be associated with two much less recognizable northern extensions of low salinity water within this core layer (Fig. 5). To the south of Australia the distribution of salinity (Fig. 5) and preformed phosphate (Fig. 7)

Fig. 8.—Depth (m) of the North-West Indian Intermediate water mass. $AA^1$, Region of minimum depth; ○, station where this water mass could not be detected.

were not consistent with one another, and the salinity gradients were too small to indicate the direction of movement of the Antarctic Intermediate water mass. From preformed phosphate values, however, two paths of movement ($CC^1$ and $DD^1$ in Fig. 7) have been selected.

## V. Distribution of the Core Layer of the North-West Indian Intermediate Water Mass

The depth of this water mass varied from about 700 m in the north-west of the region (Fig. 8) to 1300–1400 m in the south at a latitude of about 30° S. A region of comparative shallowness ($AA^1$ in Fig. 8) was found between latitude 15° and 20° S. The salinity of this core layer varied from 34·56 to 35·00‰

Fig. 9.—Salinity of the North-West Indian Intermediate water mass. 34·00 should be added to the values to obtain the actual salinity. ○, Station where this water mass could not be detected.

(Fig. 9) with the highest salinities along the north-west limit of the region, and extending eastwards along the southern coast of Sumatra and Java, and along the 20° S. parallel. The highest salinities within this core layer (Fig. 9) were associated with the lowest preformed phosphate (Fig. 10) at the north-west limit of the region. Elsewhere decreasing salinity values were paralleled by increasing

preformed phosphate values, but the tongue of high salinity water at about 20° S. was not reflected in the preformed phosphate distribution.

At most stations where the North-West Indian Intermediate water mass can be clearly distinguished as a salinity maximum on the temperature–salinity curve (Fig. 2), its depth of occurrence differed by less than 100 m from that of the major

Fig. 10.—Preformed phosphate P ($\mu$g-atom/l) of the North-West Indian Intermediate water mass. ○, Station where this water mass could not be detected.

oxygen minimum. This close correspondence in depth can be seen in Figures 11 and 12 compiled from charts in C.S.I.R.O. Aust. (1961*a*, 1961*b*, 1961*c*, 1961*d*). It is, therefore, considered probable that the major oxygen minimum layer throughout this region is associated with the spreading of the North-West Indian Intermediate water mass. On this assumption, the distribution of oxygen on this oxygen minimum layer (Fig. 13) shows that this water mass spreads further to the south off

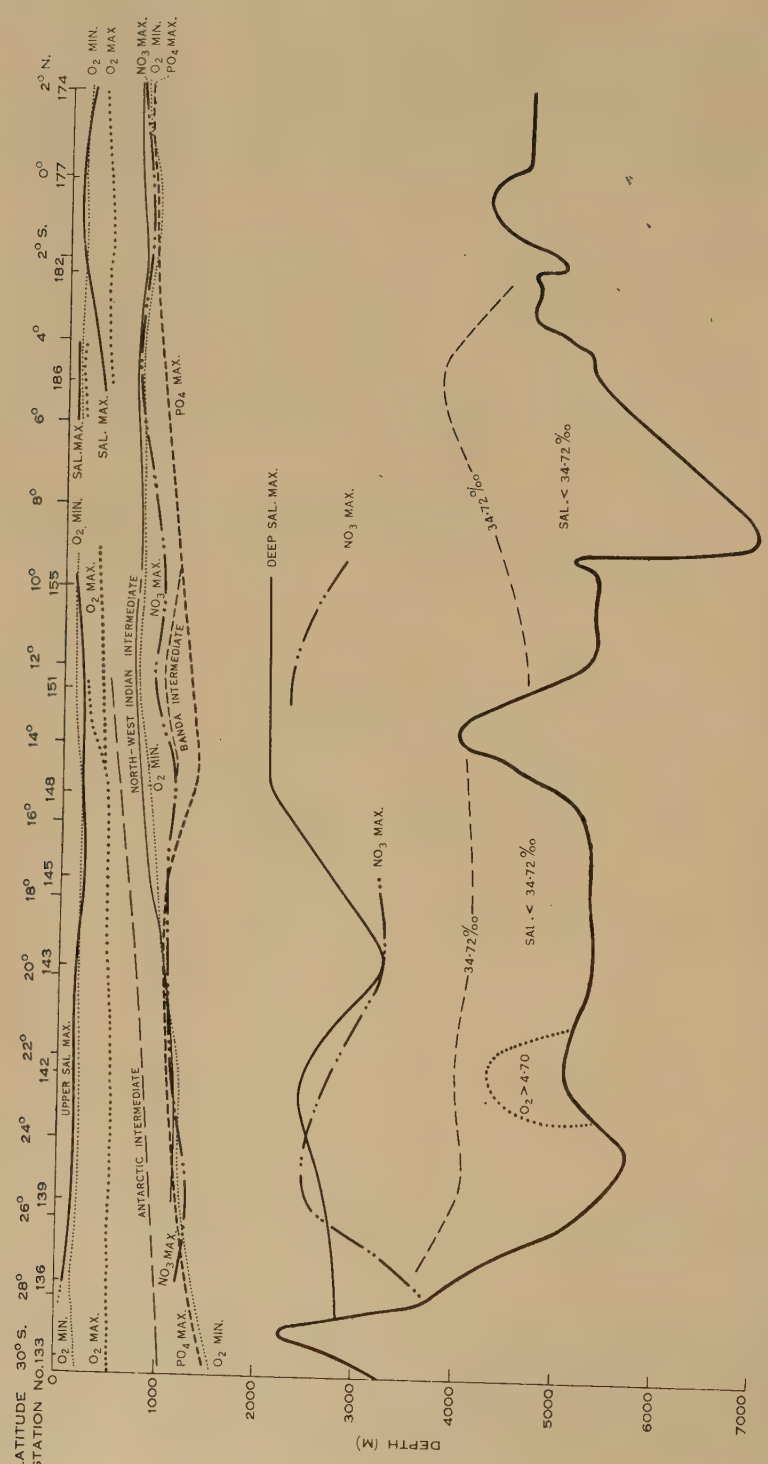


Fig. 11.—Section along the 95° E. meridian showing the depth of the major maximum and minimum layers of salinity, oxygen, phosphate, and nitrate, and of the intermediate water masses.

Fig. 12.—A section from north-west Australia to Western Java, showing depths of the layers of Figure 11.

Western Australia than the salinity (Fig. 9) would indicate. The paths of minimum oxygen content of this layer ($AA^1$ in Fig. 13) and of its branches ($A^1A^2$, $A^1A^3$, and $A^1A^4$ in Fig. 13) were situated in comparatively shallow regions (Fig. 14), and because of vertical separation were less affected by mixing with the oxygen-richer waters of the deep salinity maximum below (Fig. 11). The distribution of this

**Fig. 13.**—The oxygen values (ml/l) along the oxygen minimum layer. $A$–$A^1A^2A^3A^4$, Regions of lowest oxygen values south of 20° S.

oxygen minimum layer is also considered to be partly controlled by local biochemical processes (Wyrtki 1961*b*), and the dynamical interpretation of its distribution could, in some cases, be quite erroneous.

## VI. Distribution of the Core Layer of the Banda Intermediate Water Mass

This water mass was found throughout the region north of 25° S. at about 800–1400 m (Fig. 15). From about 800 m in the north-east it deepened to 1000 m for the greater part of its distribution north of 20° S., and then to 1300–1400 m south of this latitude. The Banda Intermediate water mass is of relatively low

salinity (Fig. 3), and the distribution of low salinity waters along its core layer (Fig. 16) shows its direction of spreading ($AA^1$, $AA^2$, and $AA^3$ in Fig. 16). The zonal paths terminating at $A^1$ and $A^2$ (Fig. 16) occurred at depths of about 1000 m (Fig. 15), but any spreading to the south (paths terminating at $A^3$ in Fig. 16) was followed by deepening to 1300–1400 m (Fig. 15) because of mixing with the deep salinity maximum layer (Fig. 6).

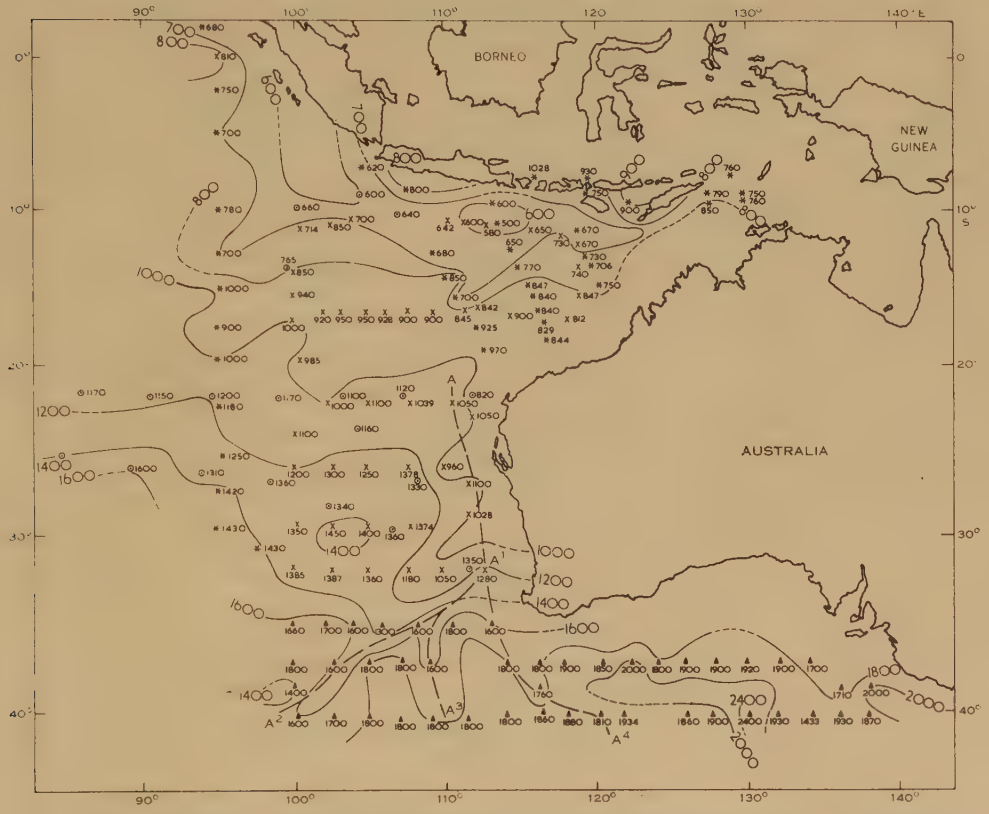


Fig. 14.—The depth (m) of the oxygen minimum layer. $A$–$A^1A^2A^3A^4$, Regions of lowest oxygen values south of 20° S. (see Fig. 13).

Along the direction of the path ($AA^1$ in Fig. 16) of the Banda Intermediate water mass higher oxygen values were found on the oxygen minimum surface (Fig. 13). This minor oxygen maximum shows up clearly in the vertical profile of oxygen in this region (Fig. 13). At station Dm 2/233/60, lying within the Banda Sea, the oxygen content at 900–1000 m was similar to that at Dm 2/208/60, and higher than that of other stations at the same depth (Fig. 17). This water of higher oxygen value is carried into the Indian Ocean by the spreading of the Banda Intermediate water mass above it.

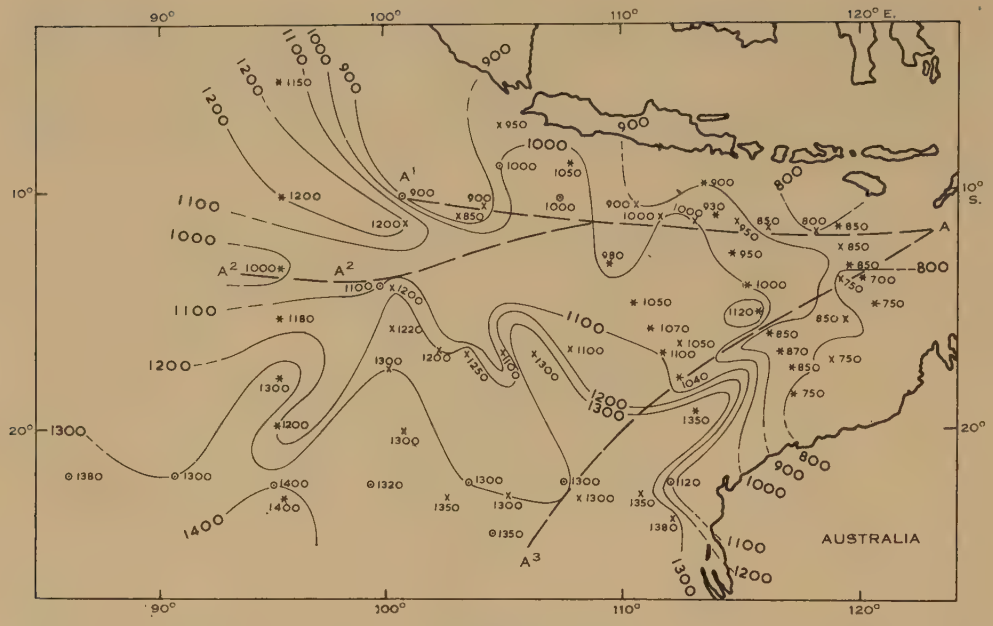


Fig. 15.—The depth (m) of the Banda Intermediate water mass. $A$–$A^1A^2A^3$, Regions of lowest salinity (see Fig. 16).

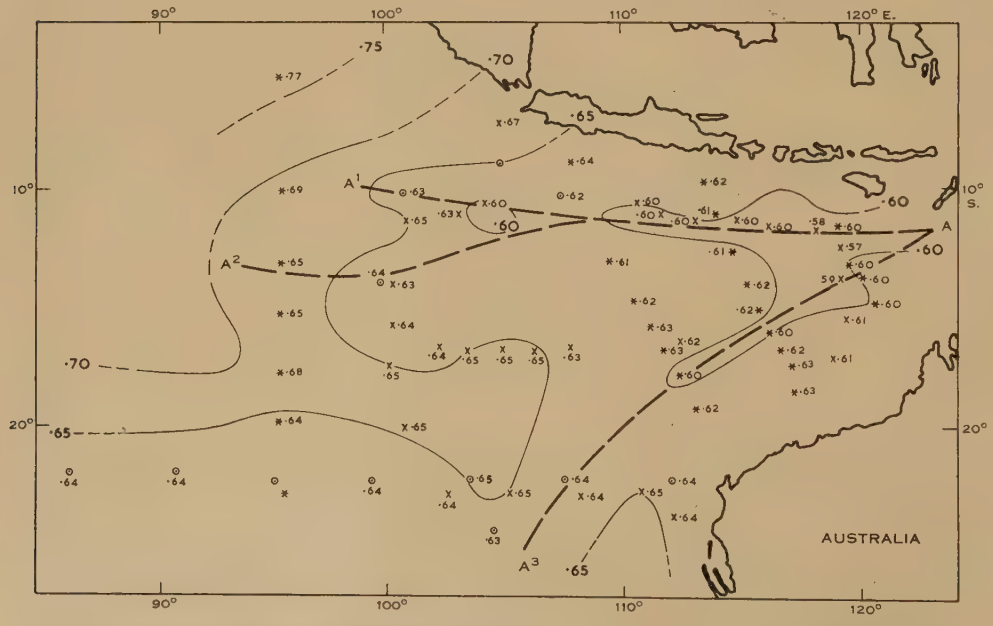


Fig. 16.—The salinity of the Banda Intermediate water mass. $A$–$A^1A^2A^3$, Regions of lowest salinity. 34·00 should be added to the values to obtain the actual salinity.

The preformed phosphate P distribution (Fig. 18) shows tongues of low values (less than 0·50 μg-atom/l) extending from the Timor Sea westwards to about 100° E., and south-westwards to about 20° S. These waters with low preformed phosphate correspond generally to the lowest salinity waters of Figure 16.

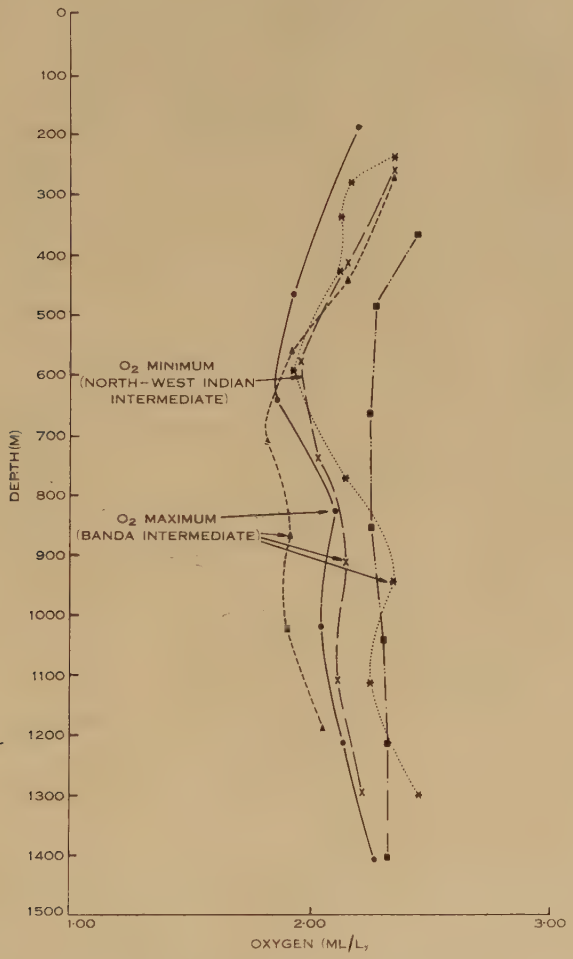


Fig. 17.—Oxygen (ml/l) profiles of selected stations. ●, Dm 2/32/59; ×, Dm 2/28/59; ▲, Dm 2/40/59; *, Dm 2/208/60; ■, Dm 2/233/60.

## VII. Mixing Processes within the Intermediate Circulation

From its initial characteristically low salinity and high preformed phosphate (*1* in Figs. 3 and 6), the Antarctic Intermediate water mass increases in salinity and decreases in preformed phosphate as it mixes with the southern portions of

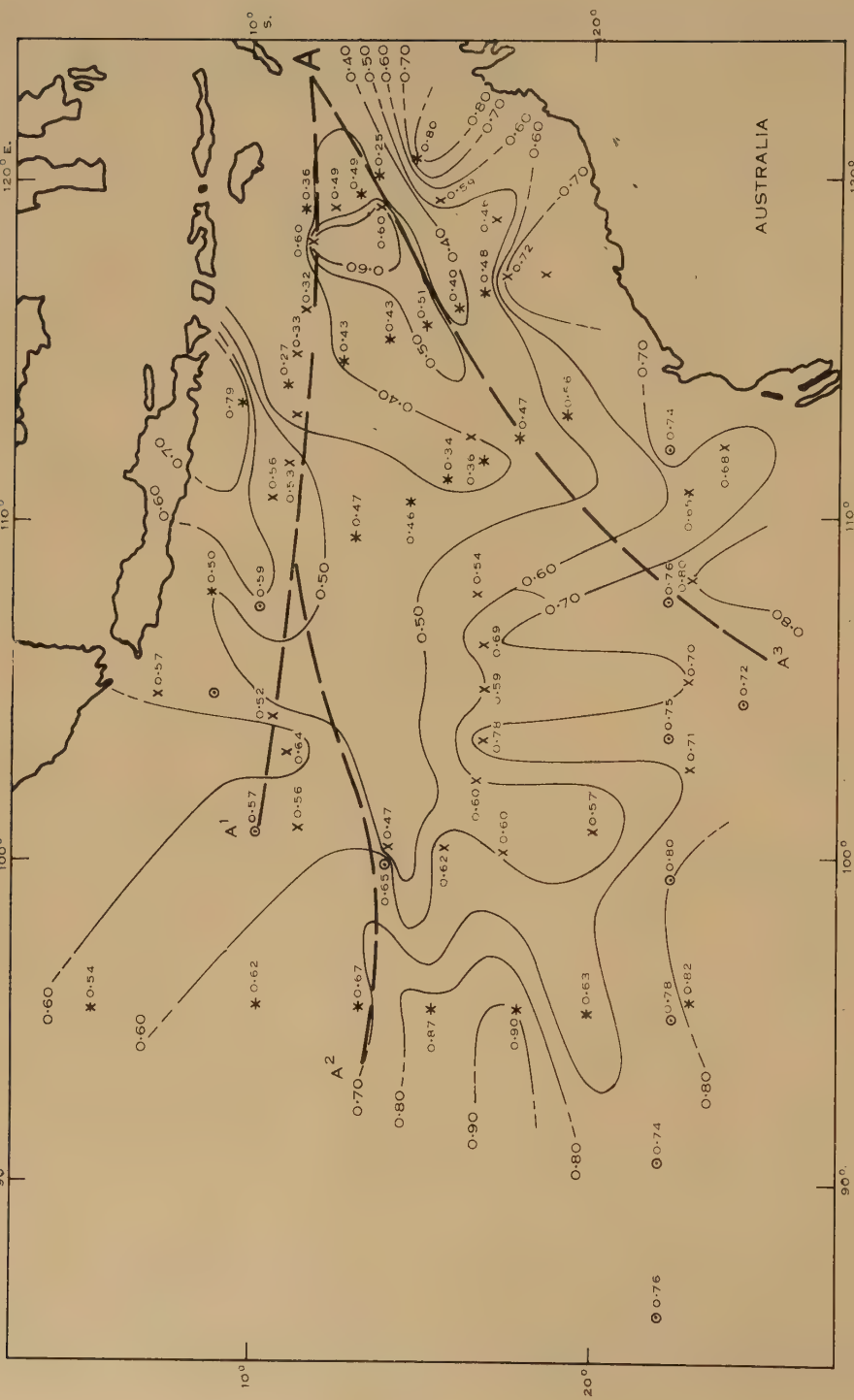


Fig. 18.—Preformed phosphate P ($\mu$g-atom/l) of the Banda Intermediate water mass. $A$–$A^1A^2A^3$, Regions of lowest salinity (see Fig. 16).

the North-West Indian Intermediate water mass below it (*E* in Figs. 3 and 6). There is also horizontal mixing at about 700–800 m with the North-West Indian Intermediate water mass to the north (*C* in Figs. 3 and 6), and finally mixing with water of the upper oxygen maximum above it (*D* in Figs. 3 and 6).

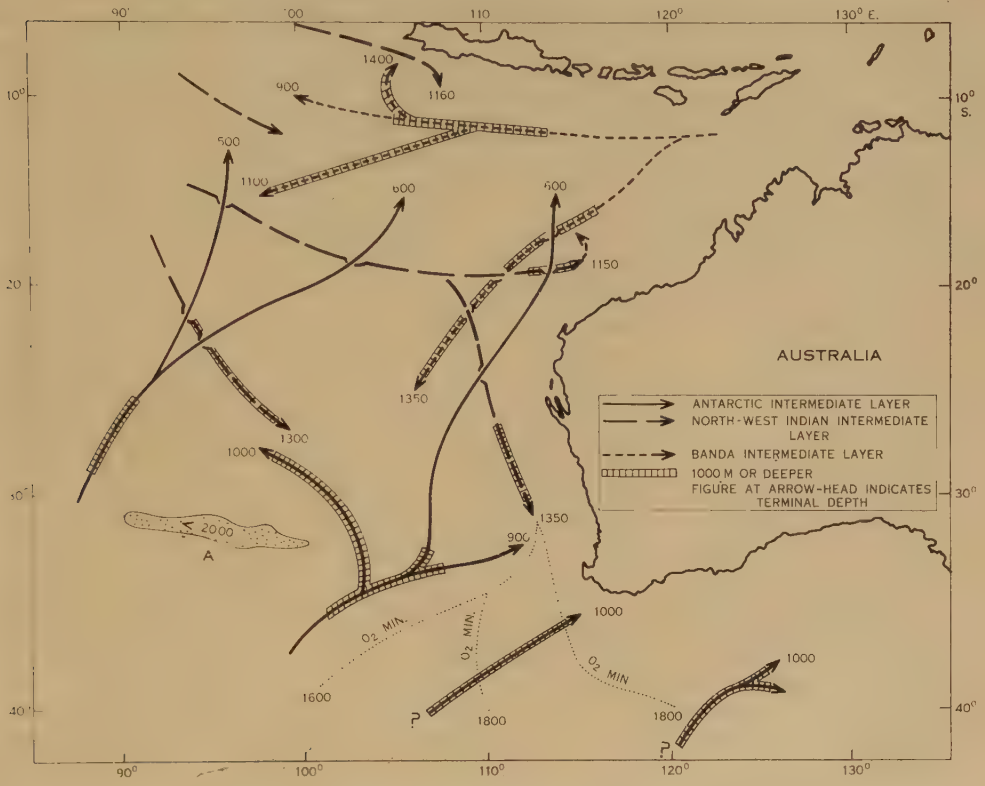


Fig. 19.—General features of the intermediate circulation of the south-east Indian Ocean.

The Banda Intermediate water mass initially has a characteristically low salinity and preformed phosphate (*2* in Figs. 3 and 6). During its spreading to the south, it mixes with the waters above it, to the south of Indonesia (*A* in Figs. 3 and 6), which are of low salinity and low preformed phosphate. There is also horizontal mixing with the North-West Indian Intermediate water mass at about 800–900 m (*B* in Figs. 3 and 6), and finally incorporation into deep waters (*G* in Figs. 3 and 6).

The North-West Indian Intermediate water mass initially has high salinity and low preformed phosphate (*3* in Figs. 3 and 6). For the greater part of its movement, during which it loses its salinity identification, it mixes horizontally with both the Antarctic and Banda Intermediate water masses (*B* and *C* in Figs. 3 and 6), and finally is incorporated into the deeper waters (*F* in Figs. 3 and 6).

## VIII. Discussion and Conclusions

Wyrtki (1961*a*), using data from *Dana* stations (Carlsberg Foundation, Copenhagen 1937) worked during October 1929 and *Albatross* stations (Bruneau, Yerlov, and Koczy 1953) worked during March 1948, was able to identify three water masses in the intermediate circulation south of Indonesia to about 10° S. These correspond in temperature and salinity with the three water masses discussed here. However, because of lack of data, Wyrtki was able to give only a limited account of their distribution. Recently Tchernia and Lizeray (1960) could identify only an Antarctic and a high salinity intermediate water mass in a section from north-western Australia to western Java during March, 1958. This apparent absence of the Banda Intermediate water mass may have been caused by a seasonal diminution of the outflow from the Banda sea at intermediate depths (Wyrtki 1961*a*). However, insufficient sampling at depths between 700 and 1500 m may have been responsible for the failure to identify this water mass in the 1958 data.

The major paths of spreading and the depths of the three intermediate depth water masses of the south-east Indian Ocean are summarized in Figure 19. The Banda Intermediate water mass, entering at about 800 m in the north-east, spreads to the west and south always at depths 200–500 m deeper than the other intermediate water masses above it. It loses its identifiable character (Fig. 2) at about 1200 miles from its region of entry. The North-West Indian Intermediate water mass spreads between the other two along several paths directed to the east, of which the most important occurs at about 20° S. From oxygen values on the oxygen minimum surface it is concluded that this water mass could spread to the south of Australia well beyond the geographical limits of its detection on temperature–salinity curves. West of Australia the Antarctic Intermediate water mass spreads northwards along two main paths; the eastern one terminates at about 15° S., and the western at about 12° S. It is probable that the submarine elevation to less than 2000 m (*A* in Fig. 19) is responsible for this bifurcation. Both branches terminate in waters of the upper oxygen maximum (*D* in Fig. 6). South of Australia spreading of this water mass could occur along two paths extending to the north-west. Because of the small gradients in salinity (Fig. 5) and in preformed phosphate (Fig. 7), the interpretation of data from this region is much less exact than elsewhere.

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# THE IDENTITY OF THE AUSTRALIAN LYMNAEID SNAIL HOST OF *FASCIOLA HEPATICA* L. AND ITS RESPONSE TO ENVIRONMENT

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*Summary*

The taxonomic literature on the Australian Lymnaeidae is reviewed, with reference to the names used for Australian snail groups. The three generic names based on Australian type species are all considered to be synonyms of *Lymnaea* Lamarck.

The specific names are discussed and new synonymies are given as a result of a comparison of type material, laboratory breeding experiments, and field observations.

It is concluded that there is only one species which acts as the intermediate host for *Fasciola hepatica* L., in both Australia and New Zealand, and that its correct name is *Lymnaea tomentosa* (Pfeiffer, 1855).

## I. Introduction

The importance of certain lymnaeid snails which act as the intermediate hosts for the common liver fluke, *Fasciola hepatica* L., has stimulated many research workers to investigate their ecology and biology.

Laboratory studies have shown that the snails alter their morphological characteristics in response to variations in environmental conditions, especially in those features which have been used as diagnostic characters for the described species.

This report gives details of these observations and the taxonomic identity of the host snail is reconsidered in relation to the observed variations.

## II. Snails Described Previously

Many names have been bestowed on various Australasian lymnaeid snails and they can be divided into two major groups. One group comprises snails with large (25 mm or more) globose shells, which have not been implicated in the transmission of liver fluke and which have been regarded by Iredale (1943, 1944) and others as forming a separate genus, *Peplimnea*. This group will not be considered in detail here, but Hubendick's (1951) view is supported that there is no justification for the separation of these forms from *Lymnaea* s.s. and in general there appears to be only a single, widely distributed species which varies greatly under environmental stress, and which should bear the name *Lymnaea lessoni* Deshayes.

The second group consists of snails with small to medium size (the largest snail recorded is 16 mm long) shells of varying form and with rather variable animal characters, which have been implicated in the transmission of *Fasciola hepatica*.

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The names which have been applied to living members of this group from Australia and New Zealand are listed below together with the type localities.

*Succinea tomentosa* Pfeiffer, 1855 (New Zealand)
*Lymnaea huonensis* Tenison-Woods, 1876 (Upper Huon River and Craycroft River, etc., Tasmania)
*Lymnaea hobartonensis* Tenison-Woods, 1876 (Hobarton = Hobart, Tasmania)
*Lymnaea launcestonensis* Tenison-Woods, 1876 (Creek near Launceston, Tasmania)
*Lymnaea subaquatilis* Tate, 1880 (River Torrens at Adelaide, South Australia)
*Lymnaea papyracea* Tate, 1880 (Penola, South Australia)
*Succinea johnstoni* Tate, 1880 (Tasmania)
*Lymnaea brazieri* Smith, 1882 (Glebe Point, Sydney, New South Wales)
*Lymnaea victoriae* Smith, 1882 (Bairnsdale, Victoria)
*Lymnaea viridula* Tate, 1882 (Murndul, Hamilton, Victoria)
*Lymnaea ampulla* Hutton, 1885 (Arthur's Pass and Lake Lyndon, South Island, New Zealand)
*Lymnaea arguta* Hutton, 1885 (River Avon, Christchurch, South Island, New Zealand)
*Lymnaea leptosoma* Hutton, 1885 (Wellington, North Island, New Zealand)
*Lymnaea pucilla* Hutton, 1885 (Auckland, North Island, New Zealand)
*Lymnaea tenella* Hutton, 1885 (River Heathcote, Christchurch, South Island, New Zealand)
*Lymnaea subaquatilis neglecta* Petterd, 1889 (Titree swamp near Launceston, Tasmania)
*Lymnaea gunni* Petterd, 1889 (South Esk River, near Launceston, Tasmania)
*Lymnaea lutosa* Petterd, 1889 (Brighton, River Jordan, Tasmania)
*Lymnaea alfredi* Suter, 1890 (Governor's Bush, Hooker Valley, South Island, New Zealand)
*Lymnaea ampulla globosa* Suter, 1891 (Tasman Valley, South Island, New Zealand)
*Lymnaea venustula* Cherry, 1896 (Headwaters of the Wimmera, Victoria)
*Glacilimnea gelida* Iredale, 1943 (Blue Lake, Mt. Kosciusko, New South Wales)
*Simlimnea aegrifer* Iredale, 1944 (Bombala, New South Wales)
*Simlimnea morbida* Iredale, 1944 (Walcha, New South Wales)

## III. Generic Classification

The most recent taxonomic studies on these snails have been those of Cotton (1942, 1943), Iredale (1943, 1944), Hubendick (1951), and Dell (1956). The first two authors admitted nearly all of the named Australian forms listed above as separate species, and allotted most of them to one of two genera, *Austropeplea* Cotton, 1942, and *Simlimnea* Iredale, 1943. One small, aberrant population was placed in a separate monotypic genus, *Glacilimnea* Iredale, 1943. However, the definition of these genera is difficult, as there is almost continuous gradation from one species to the other. The genus *Austropeplea* Cotton, 1942, with type species (original designation) *Lymnaea papyracea* Tate, was erected partly on shell characters but principally on the extreme width of the mantle border which almost covered the shell, so that the animal was unable to withdraw fully. Similar characters had been previously reported by Petterd for *Lymnaea launcestonensis* Tenison-Woods. However, specimens of *Lymnaea papyracea* Tate from South Australia, when reared under laboratory conditions, lose the expanded mantle border almost completely in a single generation, thus indicating that it is partly an ecophenotypic character, and is of no taxonomic value. Hubendick (1951) expressed a similar opinion.

*Simlimnea* Iredale, 1943, with type species (original designation) *Lymnaea brazieri* Smith, was established on shell characters only, but Hubendick (1951) has shown that these are insufficient for generic classification in the Lymnaeidae, and that the characters given for *Simlimnea* would apply equally to many lymnaeid

snails throughout the world. Similarly, the genus *Glacilimnea* Iredale, 1943, monotypic for *G. gelida* Iredale, 1943, was established on the small size of the shell (4·5 mm long) and its brown longitudinal striations. However, our observations have shown that it is common to find populations of mature specimens, 8–11 months old, with brown striated shells from 4 to 5 mm long, living in suboptimal habitats throughout eastern Australia.

Dell (1956) reviewed the New Zealand species and used *Limnaea* (*sic*) for two species and *Simlimnea* for a third. A fourth species was regarded as unidentifiable. He rejected *Myxas* and *Amphipeplea* for the common New Zealand species (*tomentosa*) on the grounds that the mantle border barely covered the edge of the shell. His use of *Simlimnea* was based on the close similarity between New Zealand and Australian specimens referred to that genus, while his reference of two species to *Limnaea* was based on (1) the fact that one was the young of the introduced *L. stagnalis*, (2) the shell shape of the other (*L. alfredi*) differed considerably from that of *tomentosa* and data on the animal characters were lacking.

However, Dell gives no additional data which would support the separation of *Simlimnea* from *Lymnaea* spp.

Thus the present authors regard all three generic names as synonyms of *Lymnaea* s.s. as was suggested by Hubendick (1951). All the Australasian Lymnaeidae are in fact referable to *Lymnaea* Lamarck, 1799.

## IV. Species Taxonomy

The status of the various named forms as "species" is a more difficult problem. As indicated previously, Cotton (1942, 1943) and Iredale (1943, 1944) admitted nearly all the named forms as full species with fairly limited geographic ranges, with the exception of a few obvious synonyms. However, Hubendick (1951) suggested that there were, in fact, only one or two widespread species which varied greatly. Dell (1956) reduced the number recognized in New Zealand to three endemic species but did not refer to Hubendick's work.

The Australian Museum collection contains a series of lots which are either holotypes, "cotypes" (i.e. mostly paratypes), or topotypes or author's homoeotypes (specimens identified as a species by the original author) of the Australian species, and we have thus been able to compare authentic specimens of the several described "species". Comparatively little authentic New Zealand material was available but Dell has adequately illustrated the New Zealand types.

In the following discussion of the species taxonomy, these authentic specimens have been examined in relation to the original descriptions and figures, and opinions expressed as to the status of the several "species" accordingly. Samples of the material studied are illustrated in the accompanying plates.

Tenison-Woods (1876) described several species of this group from Tasmania, but unfortunately his material was never illustrated. The first species described by him, *L. tasmanica*, was stated to have shells 25 mm long and to have from 5 to 8 whorls. Tenison-Woods commented on the similarity to *L. stagnalis* from Europe

and there is little doubt from the dimensions and descriptions given that it was, in fact, an introduced population of *L. stagnalis*, which presumably failed to survive, as no similar forms have been found in recent years.

Tenison-Woods also described three other species, *L. huonensis*, *L. hobartonensis*, and *L. launcestonensis*. Petterd (1889), after an examination of the Tenison-Woods types in the Hobart Museum, considered that *L. launcestonensis* and *L. huonensis* were different developmental stages of one common species. As first reviser, Petterd (1889) chose *launcestonensis* as the name for the species, which he classified as *Amphipeplea*. He considered this species to be quite different from the introduced European species *Lymnaea peregra* Mull., which occurred near Hobart. *L. peregra* was apparently the source of *L. hobartonensis*, for Tenison-Woods stated in a second paper (1879) that he was unable to distinguish the two and suggested that *L. peregra* had been introduced in water casks. This seems quite possible, for it was also introduced into New Zealand where it was given several different names. There is no evidence, however, that these populations still exist.

Tate (1880) described *L. subaquatilis* from Adelaide (at the same time introducing the nomen nudum *Succinea johnstoni* Petterd as a synonym), and commented that it was allied to the Tasmanian *L. huonensis*. The description given for the species and comparison of specimens does not allow the differentiation of the two forms. Tate (1880) also described a second species, *L. papyracea*, which he later (1885) recorded from Tasmania. This species and *L. launcestonensis* were so similar that Petterd (1889) ranked *papyracea* as a variety of *launcestonensis*, commenting that the two forms were to be found living together in the same pools near Launceston, and he could not see any difference in the animals. (Both these forms proved to have the expanded mantle border, and they were referred to *Amphipeplea* by Petterd (1889) and subsequent workers.)

Smith (1882) described two more species, *L. brazieri* from Sydney, and *L. victoriae* from Bairnsdale, Victoria. The former has a broader shell but no other significant differences from the earlier named species. *L. victoriae* differed only in minor shell characters.

Petterd (1889) regarded some of the earlier described species as synonyms but added several names of his own. He described *L. subaquatilis* var. *neglecta* which was similar in shell characters to *L. subaquatilis* and occurred in similar habitats. Petterd (1889) also named *L. gunni* from Launceston, which was nearest *L. subaquatilis* var. *neglecta*, but differed in shell outline, and the animal was not of the *Amphipeplea* type. A third species was named *L. lutosa*, which was rather similar to *L. victoriae* Smith. Paratypes of Petterd's species exhibit no significant differences from the other named forms.

Two names which appear on the list, *L. viridula* Tate and *L. venustula* Cherry, are nomina nuda as well as *Succinea johnstoni* Tate mentioned previously.

Nothing further was published of taxonomic significance until Cotton and Godfrey (1938) proposed the new name *Lymnaea aruntalis* for *L. papyracea* Tate, preoccupied by *Lymnaea papyraceus* Spix, 1827. This was later made the type species of *Austropeplea* as mentioned above.

Iredale (1943) allotted the various named forms principally to the two genera *Austropeplea* and *Simlimnea*, with relatively few names relegated to synonymy. In his account of the freshwater shells of New South Wales, he later introduced two additional names, *S. morbida* and *S. aegrifer*, but the characters given are not consistent over any geographic area, and the "species" are obviously populations of the common fluke snail (Iredale 1944). As mentioned previously, the Mt. Kosciusko population named *Glacilimnea gelida* by Iredale is also referable to this species.

The most recent consideration of the taxonomy of the Australian Lymnaeidae has been that of Hubendick (1951). Unfortunately, he had insufficient material available, which did not always enable him to draw valid conclusions. For example, he suggested that *G. gelida* was referable to *Lymnaea lessoni*. He also used the name *L. tasmanica* Tenison-Woods for an Australian species when it unquestionably applies to introduced *L. stagnalis*.

Hubendick studied preserved material from a number of Australasian localities. His conclusions were that apart from *Lymnaea lessoni* Deshayes, and some populations possibly representing introduced *L. peregra*, there were two species represented in the Australian and New Zealand faunas. One, which he called *L. tasmanica*, was more or less equivalent to all the forms listed by Iredale as *Simlimnea*. The other he classified as the New Zealand *L. tomentosa* Pfeiffer, and synonymized thereunder the several "*Austropeplea*"-like species, viz. *aruntalis* (=*papyracea*), *launcestonensis*, and *huonensis*.

Hubendick differentiated between "*tomentosa*" and "*tasmanica*" on shell characters, and the following differences were noted in anatomy: "*tasmanica*" has a large spermatheca with a short spermathecal duct and the cross section of the prostate shows a bifurcated fold, while "*tomentosa*" has a long spermathecal duct with a rather small spermatheca, while the prostate has only a simple fold.

Dell (1956) reviewed the New Zealand lymnaeid fauna and admitted only three endemic species. One of these is the introduced *L. stagnalis*. *L. alfredi* Suter appears to be either a slightly aberrant population of the common species (*tomentosa*) or possibly an introduced species (*L. truncatula* Mull.). The common New Zealand species was regarded as being *Lymnaea tomentosa* Pfeiffer, which was originally described as a *Succinea* on the basis of the shell only. Both Hubendick and Dell have shown that the type specimen is a *Lymnaea* and conforms with some New Zealand populations. Dell placed *arguta* Hutton, *ampulla* Hutton, *leptosoma* Hutton, and *globosa* Suter in the synonymy of *tomentosa* Pfeiffer.

It will be seen from the foregoing survey of the taxonomy that there have been a large number of names bestowed on a continuously variable series of populations, which it is claimed exhibit some separation into two groups on animal characters.

A number of studies have been made on the variation in morphology of fluke-host snails, without entering into the problem of taxonomy. Thus Clunies Ross and McKay (1929), using the name *Lymnaea brazieri* Smith for the species they considered the most important intermediate host in Australia, examined many snails from habitats in New South Wales, Victoria, and Tasmania. They found no sig-

nificant differences between the Tasmanian and mainland populations. Durie (unpublished data, 1950) also studied the intermediate host snails from populations in New South Wales, South Australia, Victoria, Queensland, and Tasmania. He noted the ratio of length to breadth and studied the shape and size of the spire, but found no significant differences in the shell measurements between populations from the different states. Durie also studied radular structure and found as much variation within one population as between populations from different states.

## V. Present Observations

In order to clarify the taxonomy of these snails, a study was made of 61 populations from 42 localities, collected from New South Wales, South Australia, Queensland, Victoria, and Tasmania, together with some specimens forwarded by several collaborators in New Zealand. Two extreme morphological types were recognized and both were shown to serve as intermediate hosts for *Fasciola hepatica*.

*Type A*

Shell: Ovate, glossy, brownish horn-coloured, with four slightly ventricose whorls; strongly striated longitudinally; sutures rather deeply impressed; shell stout, aperture enlarged anteriorly, ovate-pyriform in shape; aperture not more than two-thirds length of shell; columellar fold slight, inner lip broad and opaque.

Animal: Length of body, when fully extended, about 1½ times length of shell: body pigmented with fine grey to black; mantle border small, covering a very narrow strip of the edge of the shell in some specimens; tentacles flat, triangular; kidney with fold formations, lying transversely, occupying not more than one-third of the roof of the mantle cavity; shell transparent in very young specimens revealing mottled surface of mantle, in older specimens shell thicker, internal structure not visible unless shell surface is scraped off; average size of egg masses produced by fully grown specimens was 15 mm length by 4 mm diameter; gelatinous mass soft, shape very variable, usually cucumber-shaped or semi-oval, sometimes irregularly curved; usually 30–50 eggs. A typical specimen (Plate 2, Fig. 1) of this form is from "Willow Wood", Orange, N.S.W., length 13 mm, breadth 9 mm, length of aperture 8 mm.

*Type B*

Shell: Ovate, thin, fragile, light horn-coloured; with four sub-ventricose whorls; spire short, sutures moderately impressed; aperture large, ovately pyriform, occupying a little more than two-thirds length of shell; columella very thin, connected with the thin but broad inner lip, which is transparent; latter hardly distinguishable from body whorl, sometimes, however, covered by a white opaque film.

Animal: Length of body, when fully extended, about twice length of shell, only slightly pigmented with white subepidermal granulation; granules large, relatively few in number; body colour generally whitish; mantle border extremely large, covering more than half shell; tentacles flat, triangular kidney similar to type A; shell always transparent, even in very old specimens, revealing mottled surface of mantle cavity; egg masses measuring about 16 mm long, 7 mm diameter; shape

characteristically reniform, with 50–60 eggs when deposited by fully grown snails. A typical specimen (Plate 2, Fig. 4) from Hamilton, South Australia, measured 13 mm in length, 8 mm breadth, with the aperture 11 mm long.

Snails collected in the field showed great variations in shells and animals and there were many intermediates between the extreme variants described above.

Samples of the various snail populations were cultured in isolation in the laboratory and the following work was done:

(1) A morphological examination of the animals and the shells was made.

(2) Egg masses from various populations were subjected to several different environmental conditions in the laboratory.

(3) Samples of the two extreme variants were bred and their progeny observed during several generations.

(4) Observations were carried out on the ecology of different snail populations, and on their susceptibility to *F. hepatica* infection.

(5) Radulae from several populations were studied.

This paper presents the results of observations of variations in the gross morphology and macroscopic anatomy, which are usually held to be significant taxonomically.

Both types were found in field collections. Snails resembling type A are apparently more common and most specimens from the tablelands and slopes in New South Wales and from higher altitudes of Queensland conform with it, also specimens from two New Zealand localities were of this type. Type B appeared to be more frequent on the plains or at lower altitudes, generally associated with higher average temperature. The typical specimen described came from South Australia, but this type is also common in the Murray River and Goulburn Valley (Victoria) Irrigation canals, and in a few isolated localities in New South Wales near Combara and Pilliga. Similar specimens have also been seen from Kilcoy, Queensland, and from near Wellington, New Zealand.

Many mixed populations of both types and many intermediate forms were found. Populations from Greenwich Park in the Goulburn District and also from Young had semitransparent shells of medium thickness. The body was generally white and the ratio of body length to shell length was intermediate. Fully grown specimens with extremely large mantle borders were found in the Murray and Goulburn Valleys, together with thin-shelled specimens with no visible mantle border. Intermediate forms do not have a large mantle border.

It was found that the morphology of the snails apparently depends on environmental conditions. Snails which originated from one population of uniform appearance produced large animals with thin shells when grown at a fast rate under good conditions with artificial feeding, but they produced small, thicker shells when grown under poor conditions with consequent slow growth.

Snails of the type B collected from South Australia were reared under laboratory conditions for eight generations in isolated cultures. The first generation offspring were less fragile, with the outer lip stronger, and the inner lip thicker and

better developed. The length of the body was reduced, and perhaps the most striking change was the almost complete disappearance of the large mantle border. After the second generation, while the shell was still more or less transparent, the granulation of the body became finer and more dispersed in a proportion of the population. After the third and fourth generations, the shells became very similar to type A, though the body still retained slight, but distinguishable characteristic differences.

The variation within the type A populations reared in the laboratory was not great. It is possible that this morphological type is fairly constant, or that the conditions necessary for production of the B type snails were not reproduced in the laboratory. Growth rates vary widely, even in one population hatched from a single egg mass and reared in the same environment, but there are very great differences in growth rates in different environments. If well fed, the snails reached a length of 7 mm and reproduced within a month; whereas poorly fed snails from the same population, 8 or 9 months after hatching, were only 4 mm long and failed to produce eggs. When grown at a fast rate, these snails resembled type B shells during the first two months of their life, but afterwards the growth rate slowed and although they became very large later, they still retained the typical A form, with stout shells and the animals remained without large mantle borders.

One population of New Zealand snails which represented an intermediate type, as it was closer to type B in appearance and to type A in colour, was reared in the laboratory under several different environmental conditions. They followed exactly the same pattern as the Australian snails of different types. Some of the snails in the first progeny lost the black pigmentation of the body and became similar to type B from South Australia where optimum conditions were provided for a fast growth rate. Other snails from the same generation retained the original character under unfavourable conditions.

Observations on the ecology of different populations of type A and type B from Australia and New Zealand have shown that they have similar habits, egg-masses, dynamics of egg production, and hatching time of the eggs. The ecology of *L. lessoni* differs quite considerably from the results of the above observations.

Artificial infections with *F. hepatica miracidia* have shown that every population of type A and B from different localities was equally susceptible but the larvae failed to develop in any of the large numbers of *L. lessoni*, of different age and from different localities, that were tested.

Transverse sections of the prostate glands of type A and B from Australia and New Zealand did not reveal consistent differences as recorded by Hubendick (1951), and there appear to be wide variations in the length of the spermathecal duct. Hubendick (1951) showed that the spermathecal duct of the European *Lymnaea peregra* varies considerably in length, and the present observations showed that an equal amount of variability is present in the Australian species.

Comparatively little attention has been paid to the radulae of the Australasian lymnaeids. Hutton (1885) figured the radulae of several New Zealand forms, including his species *arguta*, *ampulla*, and *tenella*, as well as a radula supposedly from *Lymnaea tomentosa*. Of the first three, *arguta* and *ampulla* are considered by Dell

(1956) to be synonyms of *L. tomentosa*. The two radulae figured by Hutton showed some differences, one having a formula of 23 : 1 : 23 of which about nine were laterals, bicuspid with tricuspid and multicuspid marginals, while the other had a formula of 28 : 1 : 28 with about nine laterals, tricuspid, with the marginals "normal" but appearing to be quadricuspid in the figure. Dell has shown that Hutton's *Lymnaea tenella* is probably the young of the European *L. stagnalis*, so that it need not be considered further here. The figure of the radula of "*tomentosa*" given by Hutton is very small; no formula is given, and only a central tooth with a very small single cusp, and two bicuspid laterals with widely separated cusps, are shown. Marginals are not mentioned nor figured. Hubendick (1951) commented that Hutton had figured a typical "succineid" radula as *tomentosa*, but Hutton's figure is scarcely typical of the Succineidae, which have a very large cusp on the central tooth, usually with accessory side cusps, nothing like Hutton's figure. The next information was provided by Suter (1891) who figured the radulae of his *Lymnaea alfredi*, which had 90 rows of 16 : 5 : 1 : 5 : 16, with the central rectangular, bicuspid, the laterals tricuspid, the marginals tridentate, the last marginal minute, unidentate. Dell (1956) considered the biscuspid nature of the central tooth to be of significance, and took it as evidence of the distinction of *alfredi* as a species. However, Dell appears to have overlooked Hubendick's work, in which a number of figures of Australasian lymnaeid radulae are given. These include forms identified as "*arguta* Hutton", "*tomentosa* Pfeiffer", and "*ampulla* Hutton" from New Zealand, while "*lessoni* Deshayes", "*aruntalis* Cotton and Godfrey" and "*subaquatilis* Tate" were figured from Australia. Of these, there appear to be no significant differences among the several forms, some having unicuspid centrals (*arguta* Hutton), others a unicuspid central bearing an accessory cusp on the side (*aruntalis* Cotton & Godfrey, and *ampulla* Hutton) and one bicuspid (*tomentosa* Pfeiffer). No radula counts were given by Hubendick.

In the present study, radulae have been examined from a number of populations in Australia, and there is a good deal of variation in the count, the size of the teeth, and the shape of the cusps. Some radulae even vary in themselves, having different numbers of laterals on opposite sides. From Kilcoy, Queensland, there were 72 rows of 10+ : 10 : 1 : 10 : 10+, while the population from Hampton, New South Wales, gave a count of 17 : 10 : 1 : 9 : 17. The Great Lake, Tasmania, population has a count of 16 : 9 : 1 : 9 : 16, while that from Hamilton, South Australia, was 20 : 8 : 1 : 8 : 20, 77 rows. Most of these had unicuspid teeth, with sometimes an accessory side cusp. In the New Zealand shells available from Wellington, the formula was 17 : 9 : 1 : 9 : 17 with the central definitely bicuspid in one radula, and definitely not in another. A preparation of "*arguta* Hutton" from Lake Kimihai showed counts of 13 : 7 : 1 : 7 : 13 in one radula, with apparently a bicuspid central, and 16 : 8 : 1 : 8 : 16 in another with a unicuspid central.

Thus it is quite obvious that the radula formulae of lymnaeids of this group can vary quite a lot in precise details; however, a general picture of the radula would be that it had a central tooth with a small accessory cusp and occasionally bidentate; about 7–10 lateral teeth, which have large cusps, normally bidentate with a slight accessory cusp on the inner cusp, sometimes noticeably tridentate;

and from 10 to 20 marginal teeth, nearly always with at least four cusps and generally long and slender, the outermost marginals, however, becoming very slender and unicuspid again. The number of rows is from 70 to 90, and the whole radula is always rather small, perhaps 1½–2 mm long and ½–¾ mm in width.

The application of paper chromatography to taxonomic studies on lymnaeid snails was described by Wright (1959). Using this method, Mr. B. Wagland has examined the chromatographic pattern of mucus from snails from our colonies. Although there is insufficient material available to draw conclusions, the results obtained so far indicate a marked difference between *L. lessoni* on the one hand and types A and B on the other. The different geographical strains of the intermediate host snail do not seem to show significant differences in chromatographic patterns.

It would seem, therefore, that the difference between the type B populations, which are equivalent to the "*Austropeplea*" forms of other workers, and to "*Lymnaea tomentosa*" in Hubendick's (1951) monograph, and the type A snails (*Simlimnea* of Iredale (1943) and "*Lymnaea tasmanica*" of Hubendick (1951)) are more ecological than genetic. All the named forms therefore should be regarded as variant populations of a single very widely distributed species.

The earliest available names based on Australian material are the two proposed by Tenison-Woods (1876), *L. huonensis* and *L. launcestonensis*, but the name *tomentosa* Pfeiffer based on New Zealand material has many years priority.

Hence, *Lymnaea tomentosa* (Pfeiffer, 1855) is regarded as the correct name for the intermediate host of *Fasciola hepatica* L. in Australia and New Zealand.

## VI. Discussion of Plates

All photographs of types or other authentic specimens have been arranged in chronological sequence (in order of their description) on Plate 1. When studying the figures of laboratory specimens on subsequent plates, it is suggested that comparisons with the figures on Plate 1 will be instructive, as indicated below.

Plate 2 shows the two extreme types of shell and their offspring, from several generations of laboratory breeding. For example, compare the first generation offspring of type A (Fig. 3) with fourth generation offspring of type B (Fig. 9); compare also the parent type B shell (Fig. 4) with the paratype of *Lymnaea papyracea* Tate (Plate 1, Fig. 6) and its third, fourth, and fifth generation offspring (Plate 2, Figs. 7–11) with paratypes of *Lymnaea launcestonensis*, *L. brazieri*, and *L. subaquatilis* (Plate 1, Figs. 4, 8, and 9). Figures 14 and 15 show live snails of each type, and Figure 16 shows the first generation offspring of the B type snail, which lacks the expanded mantle border.

Plate 3 shows a series of shells originating from the Bathurst–Orange area of the Central Tablelands of New South Wales. The shells figured as 1 to 10 show the range of variation in shell form to be found in a single locality; Figures 3–10 are from a single population. Compare Figure 7 with the specimen from Lake Alexandrina (Plate 2, Fig. 12) which is intermediate between types A and B.

Plate 4 shows a series of shells from various localities in New South Wales, Victoria, and Queensland. They show that there is no real geographical variation,

but that quite large variations can occur within single populations (as for example, Figs. 1–3, or Figs. 8 and 9). Figures 10, 11, and 14 show specimens intermediate between types A and B from two widely separated localities (southern New South Wales and southern Queensland).

Plate 5 shows specimens from Tasmania and New Zealand, together with their laboratory offspring.

Compare the specimens from Lemont, Tasmania (Fig. 1) with "*papyracea*" type shells (Plate 1, Fig. 6; Plate 2, Figs. 4 and 5). The specimen from the Great Lake, Tasmania (Fig. 2) represents an intermediate type, similar to the shell from Lake Alexandrina (Plate 2, Fig. 12), but its fourth laboratory generation (Fig. 3) resembles the topotype of *L. victoriae* (Plate 1, Fig. 7) or the fourth generation of type B shell (Plate 2, Fig. 8).

It is instructive to compare any shells from New Zealand with the Australian specimens. There is striking similarity between a specimen from Lake Ngatu (Fig. 6) and one from New South Wales (Plate 3, Fig. 7), and also between another New Zealand specimen from the same locality (Fig. 5) and a shell from Tumut, New South Wales (Plate 4, Fig. 8).

Two forms of *Lymnaea lessoni*, both from New South Wales, are illustrated (Figs. 11–12) at the same magnification, representing typical sizes from field collections.

All shells photographed are now deposited in the Australian Museum, Sydney, and the register numbers are given in the explanation of Plates.

## VII. Acknowledgments

The authors are much indebted to the following officers of the McMaster Laboratory: Dr. D. F. Stewart, Associate Chief of the Division, for his helpful criticism of the manuscript, Mr. I. T. Roper for his excellent and painstaking photography. Thanks are due also to Mr. B. Wagland, for the chromatographic work, to Mr. G. C. Merritt for the histological sections, and to Mr. R. I. F. Paterson for his conscientious assistance in the breeding experiments.

Dr. L. K. Whitten and Mr. L. Price of New Zealand; Dr. T. S. Gregory, Chief of the Division; and Mr. B. Wagland kindly assisted in obtaining specimens from New Zealand.

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## Explanation of Plates 1–5

### Plate 1

All figures approximately 2× natural size. A.M. = Australian Museum.

Fig. 1.—*Lymnaea huonensis* Tenison-Woods. Probable paratype (author's homoeotype). A.M. No. A1978.

Fig. 2.—*Lymnaea hobartonensis* Tenison-Woods (= *peregra* Muller). Topotype. A.M. No. C27764.

Fig. 3.—*Lymnaea launcestonensis* Tenison-Woods. Probable paratype (author's homoeotype). A.M. No. A1978.

Fig. 4.—*Lymnaea launcestonensis* Tenison-Woods. Probable paratype. A.M. No. 1978.

Fig. 5.—*Lymnaea subaquatilis* Tate. Probable paratype (author's homoeotype). A.M. No. C506.

Fig. 6.—*Lymnaea papyracea* Tate. Probable paratype (author's homoeotype). A.M. No. C510.

Fig. 7.—*Lymnaea victoriae* Smith. Topotype. National Museum, Victoria. No. F1519.

Fig. 8.—*Lymnaea brazieri* Smith. Original topotype (part of original lot from which the holotype came, ex Brazier Collection). A.M. No. C42272.
Fig. 9.—*Lymnaea subaquatilis neglecta* Petterd. "Cotype" (=paratype). A.M. No. C27763.
Fig. 10.—*Lymnaea gunni* Petterd. "Cotype" (=paratype). A.M. No. C27761.
Fig. 11.—*Lymnaea lutosa* Petterd. "Cotype" (=paratype). A.M. No. C27762.
Fig. 12.—"*Amphipeplea launcestonensis papyracea* Tate." Specimen received from Petterd. Locality: Launceston. A.M. No. C27760.
Fig. 13.—*Glacilimnea gelida* Iredale. Lectotype (here selected). A.M. No. C22791.
Fig. 14.—*Simlimnea morbida* Iredale. Holotype. A.M. No. C51685.
Fig. 15.—*Simlimnea aegrifer* Iredale. Holotype. A.M. No. C51721.

## Plate 2

All figures approximately 2 × natural size.

Fig. 1.—Type A shell. Typical specimen and parent snail, Willow-Wood Station, Orange, N.S.W. A.M. No. C62972.
Fig. 2.—Another type A shell. Willow-Wood Station, Orange, N.S.W. A.M. No. C62973.
Fig. 3.—First generation offspring from type A parent (Fig. 1). A.M. No. C62974.
Fig. 4.—Type B shell. Typical specimen. Gill's property, Hamilton, S.A. A.M. No. C62971.
Fig. 5.—Type B shell. Another specimen, Hamilton, S.A. A.M. No. C62975.
Fig. 6.—First generation offspring from type B parent population. A.M. No. C62976.
Fig. 7.—Third generation offspring from type B parent population. A.M. No. C62977.
Fig. 8.—Fourth generation offspring from type B parent population, grown under poor conditions. A.M. No. C62978.
Fig. 9.—Fourth generation offspring from type B parent population, grown under good conditions. A.M. No. C62979.
Fig. 10.—Fifth generation offspring from type B parent population, grown under poor conditions. A.M. No. C62980.
Fig. 11.—Fifth generation offspring from type B parent population, grown under good conditions. A.M. No. C62981.
Fig. 12.—Lake Alexandrina, S.A. Shell intermediate in form between type A and type B. A.M. No. C62982.
Fig. 13.—Lake Alexandrina, S.A. Another specimen. A.M. No. C62983 (cf. Figs. 3 and 9 above).
Fig. 14.—Living type A snail, from Orange, N.S.W.
Fig. 15.—Living type B snail—typical specimen figured as No. 4 above. A.M. No. C62971.
Fig. 16.—First generation offspring of type B parent population from Hamilton, S.A., grown in laboratory under good conditions.

## Plate 3

All figures approximately 2 × natural size.

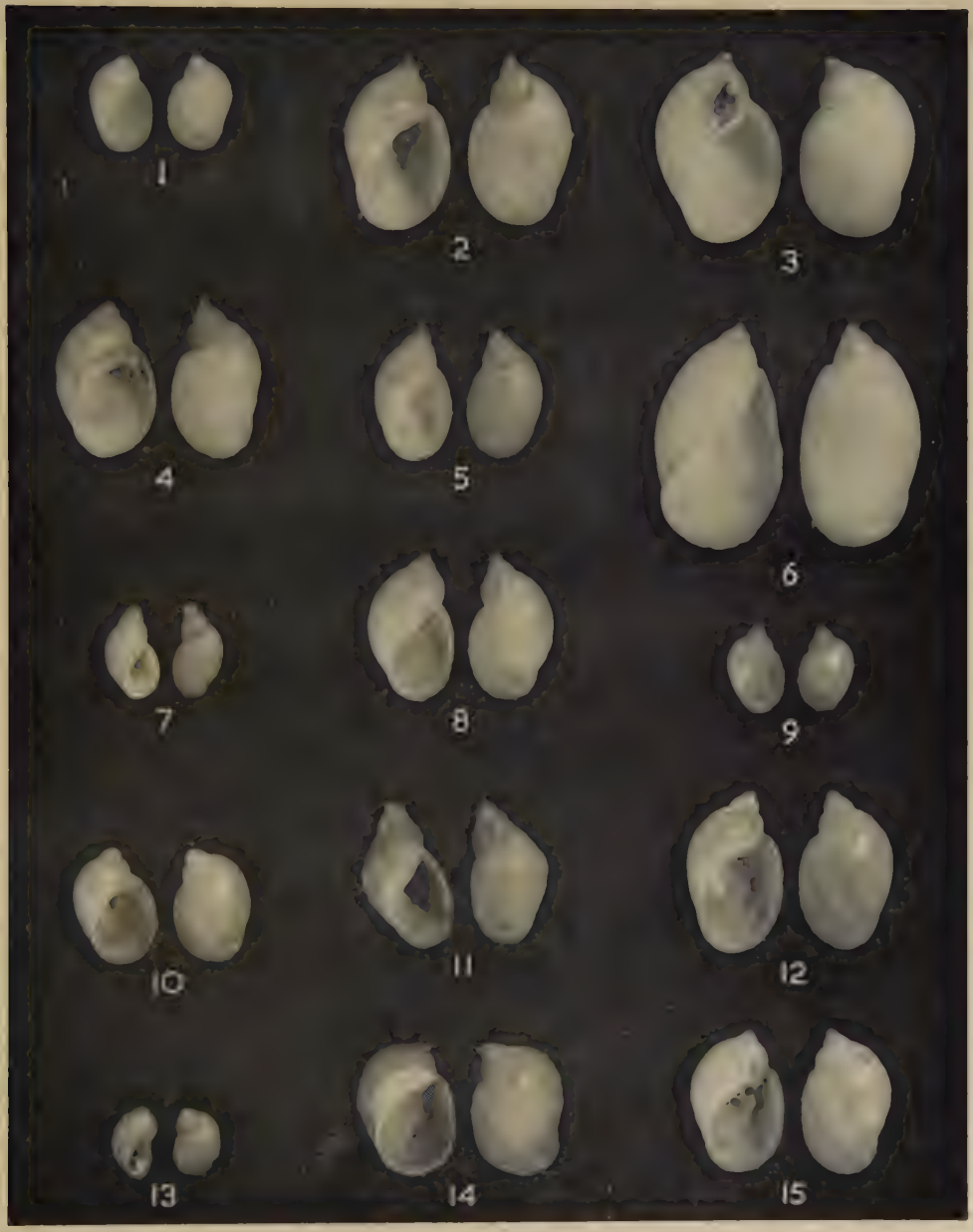
Figs 1–8.—Shells from type A population, Willow-Wood Station, Orange, N.S.W. Habitat: deep dam. A.M. Nos. C62984–91.
Fig. 9.—First generation from type A shell, figured as No. 3 above, and grown under good conditions. A.M. No. C62992.
Fig. 10.—First generation from type A shell figured as No. 3 above, grown under poor conditions. A.M. No. C62993.
Figs. 11–14.—Shells from type A population, Oberon, N.S.W. A.M. Nos. C62994–7.
Fig. 15.—Shell from type A population, Hampton, N.S.W. A.M. No. C62998.

## Plate 4

All figures approximately 2 × natural size.

Figs. 1–3.—Specimens from a single population from Young, N.S.W. A.M. Nos. C63100–2.
Figs. 4–5.—Specimens from a single population, Walcha, N.S.W. A.M. Nos. C63103–4.

THE SNAIL HOST OF FASCIOLA HEPATICA



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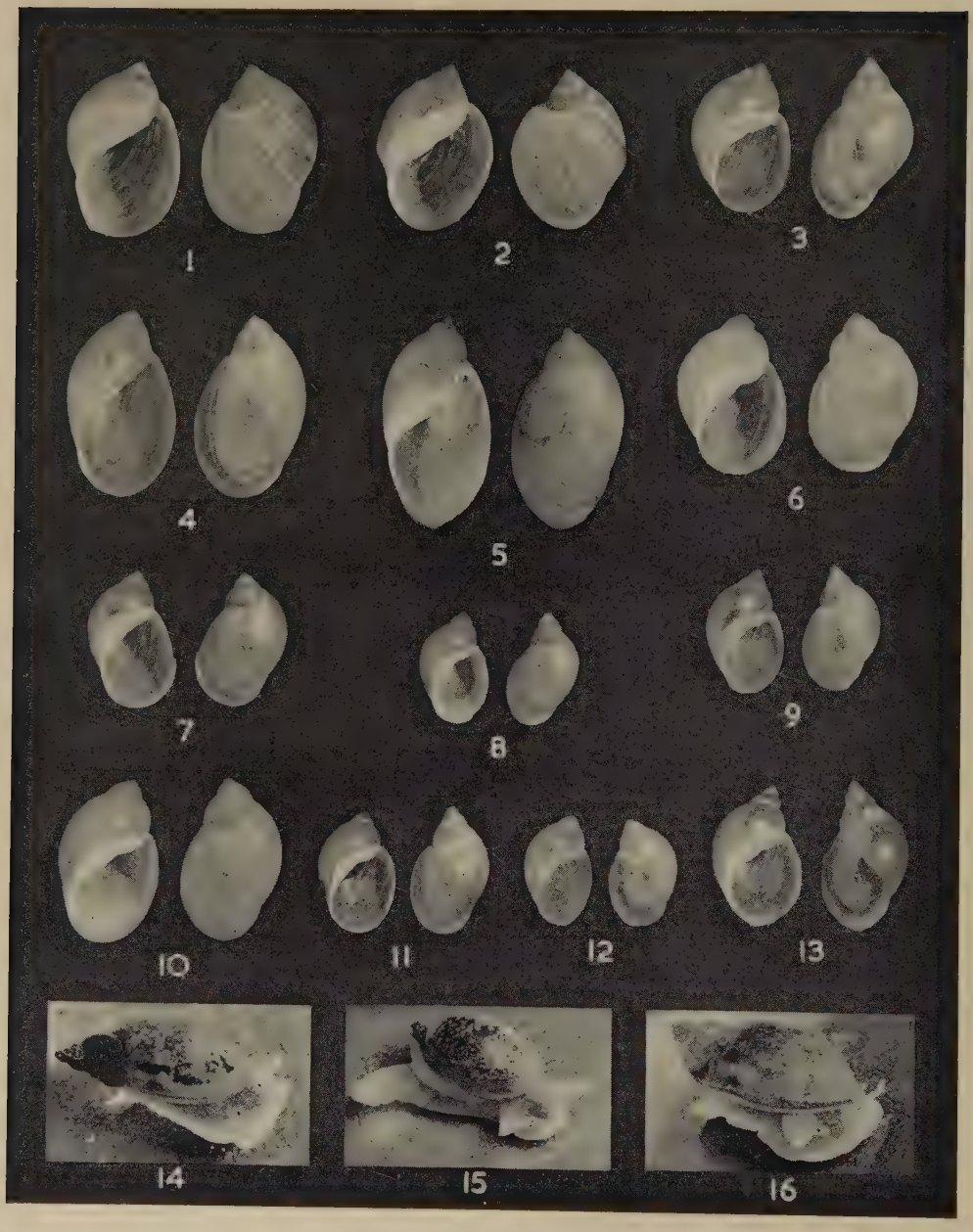

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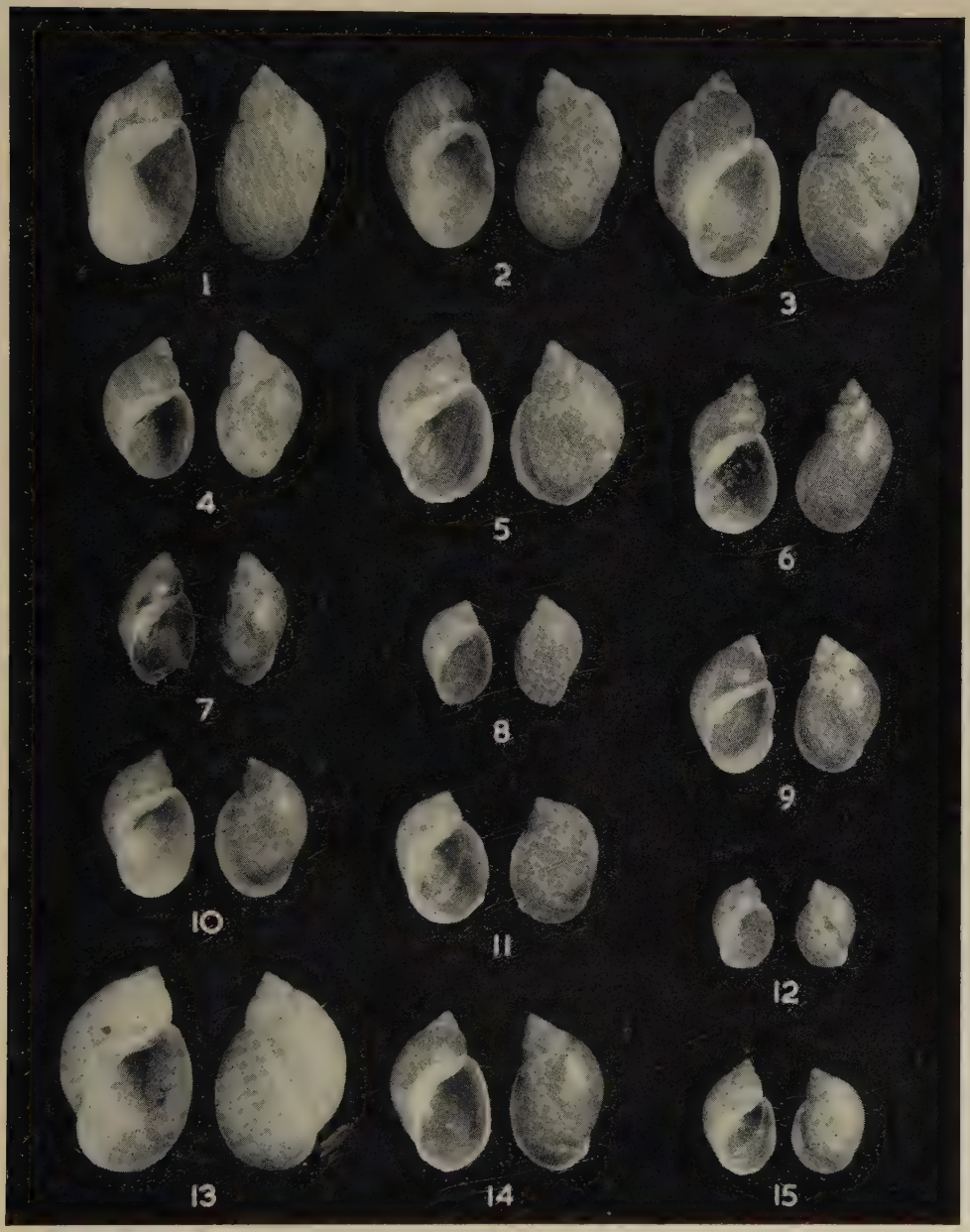

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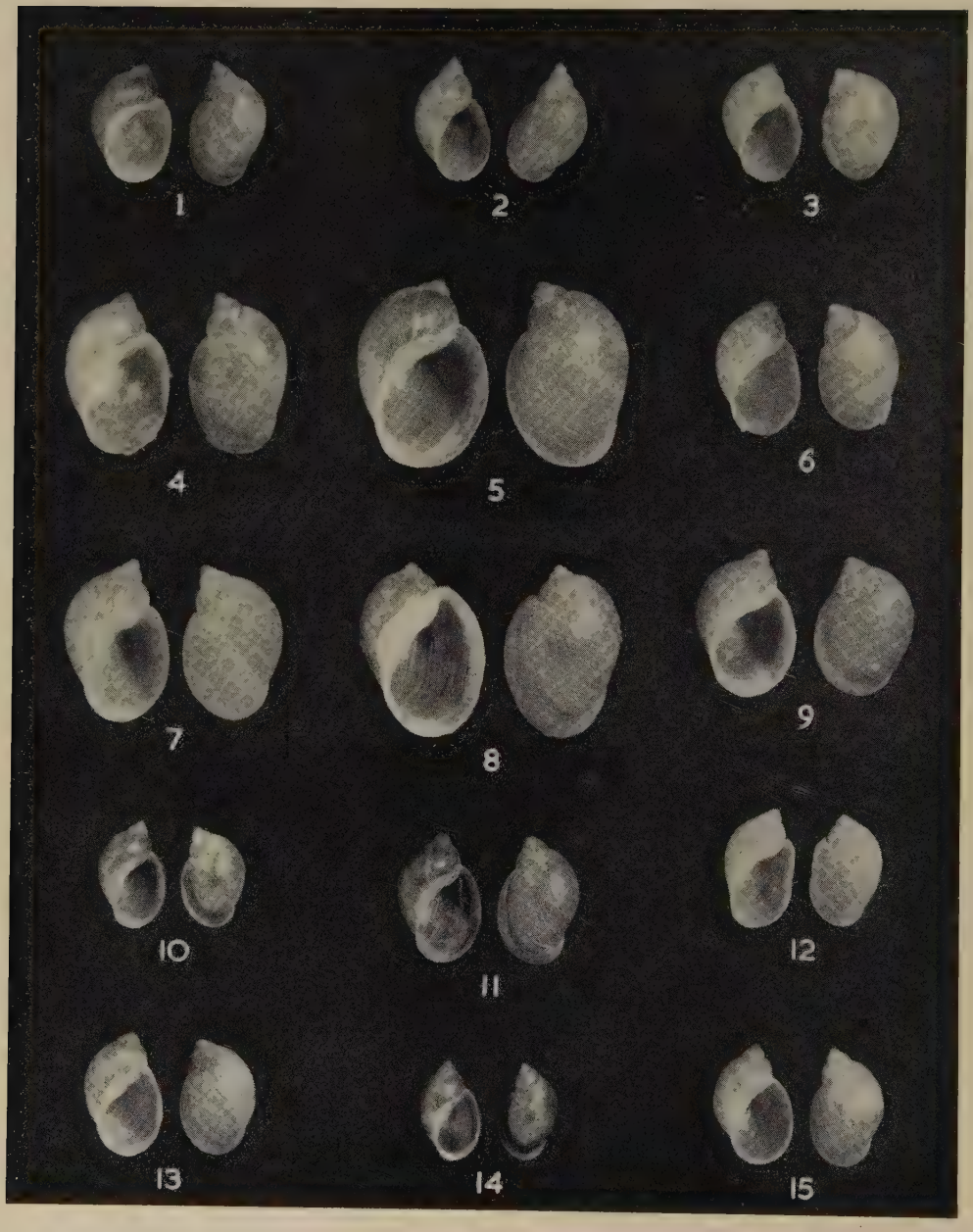

THE SNAIL HOST OF FASCIOLA HEPATICA

Figs. 6–7.—Specimens from a single population from Cooma, N.S.W. A.M. Nos. C63105–6.
Figs. 8–9.—Specimens from a single population from Tumut, N.S.W. A.M. Nos. C63107–8.
Fig. 10.—Specimen from Yuringalla Creek, Marulan, N.S.W. A.M. No. C63109.
Fig. 11.—Specimen from Greenwich Park, near Goulburn, N.S.W. A.M. No. C63110.
Fig. 12.—Specimen from Cohuna, Victoria. A.M. No. C63111.
Fig. 13.—Specimen from Nedgera Creek, Coonamble, N.S.W. A.M. No. C63112.
Fig. 14.—Specimen from Kilcoy, Qld. A.M. No. C63113.
Fig. 15.—Specimen from Stanthorpe, Qld. A.M. No. C63114.

## Plate 5

All figures approximately 2 × natural size.

Fig. 1.—Specimen from Lemont, Tas. A.M. No. C63235.
Fig. 2.—Specimen from side pools of Great Lake, Tas. A.M. No. C63236.
Fig. 3.—Specimen from the fourth laboratory generation of the parent snail No. 2. A.M. No. C63237.
Figs. 4–6.—Specimens from Lake Ngatu, north-west of Kaitaia, North Island, N.Z. A.M. Nos. C63238–40.
Fig. 7.—Specimen from Lake Wairarapa near Featherston, North Island, N.Z. A.M. No. C63241.
Figs. 8–10.—Specimens from the first laboratory generation of the parent snail No. 7. A.M. Nos. C63242–4.
Fig. 11.—*Lymnaea lessoni* specimens from Badgery's Creek, west of Sydney, N.SW. A.M. No. C63233.
Fig. 12.—*Lymnaea lessoni* specimens from Scone, N.S.W. A.M. No. C63234.

# EXPERIMENTAL STUDIES ON THE ECOLOGY OF INTERTIDAL ENVIRONMENTS AT HERON ISLAND

## II. THE EFFECT OF SUBSTRATUM

By W. Stephenson*

[*Manuscript received May* 9, 1961]

*Summary*

Different kinds of rocks were cemented to the beach rock at Heron Island both upon the open surface to permit fish browsing, and within cages to prevent it.

During a 12-month period, a negligible number of intertidal animals colonized these rocks, and their sparsity upon the surrounding beach rock is evidently not due to a substratum effect *per se*.

Minor effects of the substratum on the flora were noted. On the harder rocks the brown alga, *Ralfsia*, was a conspicuous newcomer, while green algae were best developed on the calcareous substrata.

The intensity of fish browsing was inversely related to the hardness of the rock surface, but the effect was concluded to be an indirect one, hardness affecting the thickness of the algal cover, and this, in turn, affecting the browsing intensity.

Hard concrete placed upon the beach 7 years previously was appreciably higher than the general surface, and (after making certain assumptions) it appears that rock is removed by fish browsing to a thickness of about 0·5 mm per year.

In a preliminary experiment acorn barnacles were transplanted from the reef crest to the beach rock, and a higher survival rate was observed on caged specimens.

## I. Introduction

The earlier paper of this series (Stephenson and Searles 1960) presented facts which indicated that a different biotic climax developed upon various substrates introduced on and near the beach rock at Heron Island, as compared with the beach rock itself. It appeared that this might be due to the relative softness or hardness of the substratum acting either directly, or alternatively through its effect on fish browsing. In the present work different types of substratum were introduced to the area, and the plant and animal populations were observed over a period of 12 months in conditions (*a*) allowing and (*b*) preventing fish browsing.

In the earlier paper it was suggested that the dominance of acorn barnacles at the appropriate level on the reef crest might be due to relative freedom from fish browsing. This was investigated in a preliminary manner in the present work by transplanting portions of barnacle-covered coral rock boulders to the beach rock area.

## II. Methods

The following substrata were used: basalt, hornfels, St. Lucia tuff, Stafford tuff, granite, magnesium limestone, hard beach rock, soft beach rock, concrete. To save frequent qualification, these are all referred to as "rocks".

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The quarried rocks were obtained in the Brisbane vicinity, while the concrete was made from beach sand and cement. The extreme grades of hardness of "normal" habitats were also provided in the form of (nominally) uncolonized slabs of hard beach rock and semiconsolidated crumbling beach rock respectively.

Pieces of rock were enclosed in wire-netting cages set in cement bases as in the earlier experiments (Stephenson and Searles 1960). All cages were of $\frac{1}{2}$ in. galvanized netting, and differed from the previous ones only in unimportant particulars ($\frac{3}{8}$ in. galvanized iron supports instead of $\frac{1}{2}$ in.; some wood used in construction of supports).

Into each cage either one or two types of rock were cemented, each piece being approximately 40 by 30 by 10 cm. Similar pieces were cemented to the open rock surface in the immediate vicinity. In this way comparisons could be made of the effects of different kinds of rock in both the presence and absence of fish browsing.

The cages and exposed samples were spaced at roughly metre intervals in an ESE.–WNW. direction on evenly and slightly sloping rocks, just WNW. of the lower cages of the earlier experiment (Stephenson and Searles 1960, Fig. 1). The lowest portions of the rocks (free from their concrete attachment) were approximately 1 ft above the local datum, i.e. slightly above the level of mean low water of neap tide, while the highest portions were an average of 5 in. higher. The entire samples were thus within the *Blidingia* zone of the beach rock although the upper surfaces were approaching the level at which *Calothrix* is commonly admixed with *Blidingia* (Stephenson and Searles 1960).

The hardness of the rocks was determined at the end of the experiment, using the standard material employed in Mohr's test. The rock samples were fractured and measurements made on the freshly exposed material from their centres, with results as given in the list below.

It should be stressed that the classical tests of hardness depend upon "scratchability", so that in granular material (e.g. soft beach rock) Mohr's test tends to measure the hardness of the larger granules rather than the intergranular cement. It would have been interesting to have measured resistance to pulverization, but this was not attempted. Instead verbal descriptions of the degree of the consolidation of the material are given.

The sequence of the samples (in an ESE.–WNW. direction) and their original hardnesses were as follows:

A Caged—basalt, Bundamba, Ipswich; hardness *c.* 6.
A Uncaged—as above.
B Caged—hornfels, Mt. Coot-tha, Brisbane; hardness *c.* 4.
B Uncaged—as above.
C1 Caged—tuff, St. Lucia, Brisbane; hardness 3–4.
C2 Caged—tuff, Stafford, Brisbane; hardness 3–4.
C1 Uncaged—as C1 caged.
C2 Uncaged—as C2 caged.
D1 Caged—granite, Ashgrove, Brisbane; hardness 7.
D2 Caged—magnesium limestone, south of Ipswich; hardness 4.
D1 Uncaged—as D1 caged.

D2 Uncaged—as D2 caged.
E1 Caged—hard beach rock from Heron Island, weathered by about 3 years of terrestrial exposure; hardness 3–4.
E2 Caged—soft barely consolidated beach rock from the extreme upper beach, upper surface with *Entophysalis* scraped clean; coarse grains, hardness *c.* 4, crumbling very readily.
E1 Uncaged—as E1 caged.
E2 Uncaged—as E2 caged.
F1 Caged—concrete of approximately 4 parts beach sand (almost pure calcium carbonate) and 1 part cement, weathered by about 5 years of terrestrial exposure; hardness *c.* 4.
F2 Caged—transplanted coral rock bearing barnacles *Tetraclita vitiata* Darwin.
F1 Uncaged—as F1 caged.
F2 Uncaged—as F2 caged.

The experiments were begun in the week beginning January 12, 1960, and observed on the following dates: May 29 and 30, August 8 and 9, November 5 and 6, 1960; January 22–24, 1961.

Throughout, the number of barnacles surviving upon the transplanted rocks was noted, and on the remaining samples general observations were made of the species present, with estimates of the percentages of surface covered by the different algae, the average thickness of the algal cover, and the number and sizes of animals present. These observations were restricted to the upper surfaces of the rocks, since experience had shown the difficulties of making accurate observations on vertical or overhanging faces within cages.

The terms "film", "mat", and "thick mat" were used to describe the thickness of algal cover. The first indicates a covering less than 1 mm thick, the second a covering of more than 1 mm, and the third a covering thicker than 2 mm.

The terms "dominant", "codominant", "subdominant", and "present" are used to describe the ecological status either of a given species (e.g. *Ralfsia*) or of an inextricably mixed assortment of species (e.g. blue-green algae). These descriptive terms have the same meaning as previously applied (Endean, Kenny, and Stephenson 1956; Endean, Stephenson, and Kenny 1956; Stephenson and Searles 1960) but are now capable of more precise definition. "Dominants" covered more than 50% of the occupied surface; when two entities each covered equal areas summating to more than 50% of the occupied total they are described as "codominants". "Subdominants" occurred in the presence of dominants, but only occupied 10–40% of the area. The term "present" is used when less than 10% of the area was occupied.

No attempt was made in the present work to determine the amount of chlorophyll per unit area of rock, for the following reasons:

(1) Because of the smallness of the experimental surfaces collection of the necessary triplicate samples would have caused too much disturbance to the overall picture.

(2) Some rocks (e.g. granite) were too hard to permit effective collection of the entire surface layers.

(3) Some rocks (e.g. soft beach rock) would have completely crumbled on an attempted collection of those algae which penetrate their substance.

(4) The method of determination previously used (Stephenson and Searles 1960, p. 256) has inherent inaccuracies, and the results which were obtained previously were less revealing than those obtained by general observations.

## III. Results

### (*a*) *Species Present*

Fauna

| | |
|---|---|
| GASTROPODA | *Cerithium moniliferum* Kiener |
| | *Siphonaria australis* Quoy & Gaimard |
| CIRRIPEDIA | *Tetraclita vitiata* Darwin |

Flora

| | |
|---|---|
| ALGAE | |
| CYANOPHYTA | *Aphanothece* sp. |
| | *Arthrospira* sp. |
| | *Calothrix crustacea* Thuret |
| | *Chroococcus* sp. |
| | *Dermocarpa* sp. |
| | *Lyngbya aestuarii* (Mertens) Liebman |
| | *Microcoleus chthonoplastes* Thuret |
| | *Oscillatoria nigroviridis* Thwaites in Harvey |
| | *Placoma vesiculosa* Schousb. |
| | *Rivularia atra* Roth. |
| CHLOROPHYTA | *Blidingia minima* (Naegeli in Kuetzing) Kylin |
| | *Cladophora* sp. |
| | *Enteromorpha* sp. |
| | *Monostroma* sp. |
| PHAEOPHYTA | *Ralfsia* sp. |
| RHODOPHYTA | *Erythrotrichia* sp. |

Mr. Searles, in identifying the samples, has noted with reference to Stephenson and Searles (1960):

(1) *Aphanothece* sp. was previously misidentified as *Synechococcus*.

(2) *Microcoleus* was previously misspelt as *Micrococleus*.

(3) *Enteromorpha*—probably only one species has been present throughout.

### (*b*) *Changes in Flora and Fauna*

Details of a few typical observations are given in Appendix I. Abbreviated data on the flora and fauna are given separately below.

(i) *Flora.*—Data are given in Table 1 in which non-calcareous and calcareous rocks are separately referred to. The former comprise basalt, hornfels, St. Lucia tuff, Stafford tuff, and granite, while the latter comprise magnesium limestone, hard beach rock, soft beach rock, and concrete.

It will be noted that the flora of these two types of rock differed in the frequent presence of *Ralfsia* on the non-calcareous rocks and in the increased importance of green as against blue-green algae on calcareous rocks.

TABLE 1

CHANGES IN FLORA

| Months* | State† | Conspicuous Species | Thickness of Algal Cover | Intensity of Fish Browsing |
|---|---|---|---|---|
| 4½ | U | Blue-greens dominating and *Ralfsia* present on 5 non-calcareous rocks<br>Greens dominant, blue-greens subdominant on 4 calcareous rocks | Films on 5 non-calcareous rocks and magnesium limestone<br>Mats on 2 beach rocks and concrete | No toothmarks on basalt, hornfels, and granite; few on tuffs, moderate to heavy on 4 calcareous rocks |
| | C | Blue-greens dominant in 7 cases<br>On granite and concrete, blue-greens and greens codominant | Films on 2 tuffs, granite, magnesium limestone, and 2 beach rocks<br>Mats on basalt, hornfels, and concrete | |
| 7 | U | Blue-greens and *Ralfsia* codominant on basalt, hornfels, and granite<br>Blue-greens dominant, *Ralfsia* present on 2 tuffs<br>Greens dominant, blue-greens subdominant on 4 calcareous rocks | As uncaged of 4½ months | No toothmarks on 5 non-calcareous rocks, slight browsing on concrete, moderate on soft beach rock, heavy on magnesium limestone and hard beach rock |
| | C | Blue-greens and *Ralfsia* codominant on granite and St. Lucia tuff<br>Blue-greens dominant, *Ralfsia* subdominant on basalt, hornfels, Stafford tuff, and magnesium limestone<br>Greens and blue-greens codominant on beach rocks and concrete | Films on granite, St. Lucia tuff<br>Mats on basalt, hornfels, Stafford tuff, and magnesium limestone<br>Thick mats on 2 beach rocks and concrete | |

* Time elapsed since the start of the experiment. † U, uncaged; C, caged.

TABLE 1 (*Continued*)

| Months | State | Conspicuous Species | Thickness of Algal Cover | Intensity of Fish Browsing |
|---|---|---|---|---|
| 9½ | U | Blue-greens and *Ralfsia* codominant on basalt and granite<br>Blue-greens dominant, *Ralfsia* subdominant on hornfels, the 2 tuffs, and magnesium limestone<br>Greens dominant, blue-greens subdominant on 2 beach rocks. Blue-greens dominant, greens subdominant on concrete | Films on basalt, hornfels, St. Lucia tuff, and granite<br>Thin mats on Stafford tuff, magnesium limestone, and concrete<br>Thick mats on 2 beach rocks | No toothmarks on 5 non-calcareous rocks, moderate to heavy browsing on the remainder |
| | C | Blue-greens and *Ralfsia* codominant on granite<br>Blue-greens dominant and *Ralfsia* present on basalt, hornfels, 2 tuffs, and magnesium limestone<br>Greens dominant, blue-greens subdominant on 2 beach rocks and concrete | Films on granite, and St. Lucia tuff<br>Mat or film on basalt, hornfels, Stafford tuff, and magnesium limestone<br>Thick mats on 2 beach rocks and concrete | |
| 12 | U | Blue-green algae dominant, *Ralfsia* present on basalt, hornfels, 2 tuffs, and granite<br>Blue-green dominant on magnesium limestone<br>Blue-greens dominant, greens subdominant on concrete and hard beach rock<br>Half dominated by green algae, half bare on soft beach rock | Films on 5 non-calcareous rocks<br>Mats on 4 calcareous rocks | No toothmarks on basalt and hornfels, slight browsing on granite and concrete, moderate on 2 tuffs, heavy on magnesium limestone and 2 beach rocks |
| | C | Blue-greens dominant, *Ralfsia* present on non-calcareous rocks (except Stafford tuff)<br>Blue-greens dominant on magnesium limestone<br>Blue-greens dominant, greens subdominant on 2 beach rocks and concrete | Films on basalt and granite<br>Mats on hornfels, St. Lucia tuff, magnesium limestone, and 2 beach rocks<br>Thick mats on Stafford tuff and concrete | |

The tabular results omit reference to the occasional instability of the algal cover particularly when this had attained the thickness of a mat. Such instability in the form of "cracking" or "lifting" of the mats occurred on caged hornfels after 4½ months and again after 7 months and on most of the thicker covers of the caged samples from then onwards.

(ii) *Fauna.—Cerithium* entered all cages during the January to May period and in some cases became abundant (hornfels, and the two tuffs). It was suspected that entry was at random and that *Cerithium* reduced the area and thickness of the algal coverings. But for this, bigger differences might have been expected between caged and uncaged samples in the thickness of cover.

From May onwards *Cerithium* was removed from all cages at approximately fortnightly intervals, so that the population only rarely exceeded 200 per cage. These were mostly on the beach rock bases of the cages, and appeared to have a negligible effect upon the experimental surfaces.

A single small specimen of *Siphonaria* (3 mm greatest diameter) was noted on the uncaged sample of magnesium limestone in August (i.e. after 7 months). Three specimens (up to 7 mm greatest diameter) were noted there in November (i.e. after 9½ months), and had disappeared by January (12 months).

Otherwise, excluding the microfauna within the algal mats, no animals were noted on the experimental rocks. A careful search was made for minute but macroscopic barnacles and oysters, but none were observed.

### (*c*) *Effect of a Year's Immersion upon the Rocks Themselves*

Changes were noted only with magnesium limestone and soft beach rock and in both cases the degree of consolidation rather than hardness in the classical sense was affected.

The superficial layers of the magnesium limestone were penetrated by algal filaments and the surface was so softened that the outer boundary of the rock (and hence the degree of penetration) was difficult to determine. The sludge-like surface presumably was composed partly of original rock and partly of mud trapped in the algal filaments. The rock was appreciably de-consolidated well below the depth of algal penetration, particularly in transverse sheets extending inwards from the vertical faces of the slabs. It seems probable that the effects are due to chemical rather than biological action. Their present importance is that the magnesium limestone, from being a superficially hard rock, became during the course of the work superficially soft. This could explain why initially (after 4½ months) this rock carried only films of algal growth, but later carried mats.

In contrast the surface of the soft beach rock was slightly "case-hardened". The depth of this effect (*c.* 5 mm) was approximately the same as the penetration of algae, and much less than the depth of seawater penetration.

### (*d*) *Immediate Effects of Removal of Caging Wire*

On January 23, 1961, the wire forming the upper surface of the cages was removed. After 24 hours fish toothmarks were observed on all the previously caged

samples, with densities of browsing as follows: basalt and granite, slight; the remainder, moderate to heavy. These densities were roughly proportional to the thickness of the algal cover prior to the removal of the wire.

### (*e*) *Survival of* Tetraclita

Originally the uncaged sample bore 52 living *Tetraclita*, and the caged sample 53. All survived until August (7 months) but by November (9½ months) 2 of the caged and 2 of the uncaged animals had died. By January (12 months) only 43 of the caged specimens (81%) and 16 of the uncaged (31%) had survived. Evidently caging increases the chances of survival.

## IV. Discussion

In the previous paper (Stephenson and Searles 1960) it was shown that the middle and lower levels of the beach rock at Heron Island are intensely browsed by fish. However, prevention of browsing by enclosure within cages did not greatly influence the specific composition of the beach rock biota. The species present are dominated by blue-green algae (mainly *Calothrix*) and green algae (mainly *Blidingia*), the fauna being remarkably circumscribed and sparse. Noteworthy in particular is the absence of the various species of acorn barnacles and oysters characteristic of mainland beaches (Endean, Kenny, and Stephenson 1956) and of the reef crests of many of the islands off the coast (Endean, Stephenson, and Kenny 1956; Stephenson, Endean, and Bennett 1958).

In the earlier work of the present series incidental observations were made upon different kinds of substrata which had been introduced previously to the area. These observations indicated a "substratum effect" on the algae and also on the intensity of fish browsing. In the present work a series of rocks were introduced to the beach rock area and observed over a 12-month period. It was hoped to confirm the "substratum effect" as regards algae, and also that normal intertidal animals (e.g. acorn barnacles and oysters) might settle upon the introduced rocks. To prevent the possibility of their early removal by the browsing of fish, caged samples of rocks (as well as uncaged ones) were employed.

### (*a*) *Fauna*

The results of animal settlement have been given already. *Cerithium* entered all cages during the first 4½ months of the work, but was not present on any of the uncaged samples. It appeared in some cages during the previous work (Stephenson and Searles 1960) and it was then concluded (1) that the species is possibly introduced bodily from adjacent areas by waves and (2) that the enclosed and irregular environment of a cage provides suitable conditions for its continued existence. The present results support these conclusions. Frequent removal was undertaken to limit the effects of its grazing.

Apart from *Cerithium*, the only rock-dwelling animals noted were a few small specimens of *Siphonaria* on one of the exposed samples (magnesium limestone).

Even these were present only for a short while and it was suspected that they had been removed by the increase in fish browsing during the summer months.

The failure of animals to settle cannot be due to the browsing of rock surfaces by fish, firstly because half the samples were protected against browsing, and secondly because the harder rocks showed either no fish toothmarks or only a few, and then only in summer.

It seems unlikely that potential surfaces for animal attachment were too densely colonized to permit of their settlement because for at least three-quarters of the year only algal films (blue-greens and *Ralfsia*) were present on most of the rocks (including caged rocks).

It is possible that the rock surfaces were unsuitable for settlement in some not very obvious respects. Wilson (1932, 1948, 1951, 1952, 1953*a*, 1953*b*, 1954, 1955, 1960) has demonstrated that substrata of particular types are required for the settlement of polychaete larvae, and this work has been extended to other groups (see Jaegersten 1940; Silén 1954; Schetema 1961). In the present case, however, one might expect on general grounds that "bare" rocks, covered by these algal films, would be a suitable type of substratum for settlement of barnacles or oyster larvae. Knight-Jones and Stephenson (1950) and Knight-Jones (1953) have shown that barnacle larvae settle by preference adjacent to adults of the same species (see also Cole and Knight-Jones 1949). No settlement of *Tetraclita* occurred on the transplanted rocks bearing adults, either in the open or in cages.

It seems likely that the absence of settled stages of the normal intertidal fauna during the present experiment was mainly because no larvae of the appropriate species were present in the area. The dense coral population of the reef flat feeds upon zooplankton (Yonge 1930, 1931, 1940, 1957, 1960; Abe 1938) and is no doubt effective in removing it as Odum and Odum (1955) have inferred. Coral predation upon planktonic larvae at situations like Heron Island could partly explain the absence of barnacles and oysters from the beach rock and their restriction to the reef crests.

Newman (personal communication) has drawn attention to the extreme rareness of young barnacles in coral-dominated areas, and certainly this applied to the Capricorn Group. It is possible that reef-dwelling acorn barnacles have a low reproductive rate or that they reproduce only at infrequent intervals. Conceivably the present experiment was of too short a duration to show any settlement even if optimal conditions for settlement had been provided.

Even if larvae were produced, escaped the attention of the corals, and settled on the beach rock, there would be further hazards from the browsing of fish and other organisms. The present results indicate a differential mortality of uncaged as against caged specimens of *Tetraclita* kept for a year in the beach rock area. Newman (1960), quoting ideas which arose during the earlier work by Stephenson and Searles (1960), has also stressed the importance of fish browsing in the tropical West Pacific in reducing the barnacle populations. He rightly considers that systematic rasping of algal-bearing rocks is likely to have the most important effects by preventing the establishment of young barnacles. The present work shows that even if barnacles survived these hazards, they would be adversely affected at the adult stage by fish.

### (*b*) *Flora*

(i) *Effects of Caging.*—The present results confirm the previous work (Stephenson and Searles 1960) in showing that enclosure in fish-proof cages leads to a thicker growth of algae. This was especially obvious for the harder rocks (basalt, hornfels, tuffs, and granite) and since in these cases the uncaged rocks showed negligible effects of fish browsing the difference is probably due to the shelter the cages provide from wave action. The algae did not appear to penetrate the surface layers of the hard rocks to any extent and so a relatively greater effect of wave action would be expected here, as against with the softer rocks.

Caging also leads to an increase in the importance of blue-green algae, as against brown and green algae, and again shelter from wave action is possibly responsible. It should be stressed that, because of the protection by the reef crest, the area as a whole is only exposed to slight wave action—excepting during the infrequent cyclones.

(ii) *Effects of Substratum upon the Flora.*—Throughout, the flora was dominated by a variety of blue-green algae, of which the commonest species was probably *Calothrix*. The less important species differ with the nature of the substratum, and in five of the experimental rocks (basalt, hornfels, the two tuffs, and granite) *Ralfsia* was conspicuous, and occasionally attained codominance. (This species was not observed in the previous experimental areas, although it was present upon the concrete bases of iron stakes upon the beach rock and was recorded as one of the "black encrusting filamentous algae".) The presence of *Ralfsia* is evidently related to hardness of the substratum and was best developed on basalt and granite respectively. *Ralfsia* was present throughout the observations, and hence is not an annual, nevertheless it was of greatest significance in August. Its presence during 1960 upon concrete which had been placed on the beach rock 7 years previously, shows that it is not merely a sere in the algal succession. It is best regarded as part of a seasonally fluctuating climax.

In contrast to the five introduced rocks, the two beach rocks and the concrete did not develop *Ralfsia*, but instead, a variety of green algae (*Enteromorpha*, *Blidingia*, *Cladophora*, and *Monostroma*). Their combined flora of blue-green and green algae was reasonably comparable to that of the open beach rock, except for the greater importance of the blue-green algae. It must be concluded that the occurrence of *Blidingia* as a zone-forming dominant upon the beach is basically due to the nature of the substratum. It is uncertain whether the main factor is the relative softness or the calcareous nature of the rock. Unfortunately the results with the magnesium limestone do not give any pointer, because this material became noticeably softer some months after being cemented in position. Experiments with a different range of experimental substrata are required to elucidate this point.

(iii) *Seasonal Changes.*—Although the experiment was of too short a duration to distinguish clearly between stages in successions and seasonal changes, the following are strongly suspected to vary seasonally: (1) *Ralfsia*—of greatest importance in winter; (2) Blue-green algae—of greatest importance in summer; (3) Fish browsing—of greatest intensity in summer.

(iv) *Fish Browsing.*—Throughout, browsing intensity was greater on the softer rocks. On the hard rocks no browsing was noted on exposed samples of basalt and hornfels, and very little (and that only in summer) on granite.

In addition to hardness on the Mohr scale, other factors are involved because with four rocks of roughly the same hardness (the two tuffs, hard beach rock, and concrete) browsing intensities differ. Little browsing occurred on the tuffs, somewhat more on the concrete, and heavy browsing on the beach rock.

After removal of the cage roofs, browsing occurred on all the previously enclosed samples. This indicates that neither the hardness nor the chemical nature of the rock is the paramount factor.

Probably the density of algal growth is the main consideration. On the softer calcareous rocks this growth is most vigorous and browsing is most intense. Not only superficial but also penetrating algae are removed, the rock surface being scraped away in the process. Apparently the algae cannot penetrate hard rocks (nor can the fish scrape away the superficial rock), and the algal cover is normally too thin to encourage browsing. When the harder and also the non-calcareous rocks develop a denser algal cover, either as a result of the protection from the "elements" within a cage or as a result of more vigorous summer growth, fish browse on them.

It should be noted that although the softer calcareous rocks (including the "weathered" magnesium limestone) were browsed more intensively than the remainder, they still carried a heavier standing crop of algae.

The relatively soft "calcareous" concrete used in the present experiment was slightly browsed. Considerably harder concrete, which was used in the beach rock area in the form of bases for iron stakes, is even less subject to fish browsing. This harder material had been in position for 7 years when the present work concluded, and during this period the edges had become noticeably higher than the surrounding beach rock. The indications were that this was due to depression of the surrounding surface rather than breaking away of the edges of the concrete. Measurements upon two bases in the *Calothrix* zone gave an average difference in height of 5·3 mm (mean of 16 measurements, range 2–12 mm) and upon a single base in the *Blidingia* zone an average of 7 mm (mean of 5 measurements, range 5–9 mm). These crude measurements indicate the possibility that the surface of the beach rock is being lowered at a rate of about 0·5 mm annually. While mechanical erosion and chemical solution cannot be excluded, the continual removal of surface rock by algal feeding fish must be a major factor in this lowering. Newman (1960) also stressed the role of the fish and states (p. 91): "their raspings may be responsible for an appreciable amount of erosion of limestone reefs".

## V. Acknowledgments

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## APPENDIX I

### EXAMPLES OF DETAILED RESULTS

These results were obtained on November 5 and 6, 1960.

| | | | |
|---|---|---|---|
| A | (Basalt) | Uncaged | 50% *Calothrix* film, also containing *Dermocarpa*<br>50% *Ralfsia*<br>*Blidingia* present<br>No fish toothmarks |
| | | Caged | 50% *Calothrix* thin mat, also containing *Lyngbya* and *Microcoleus*<br>45% thin film *Calothrix* etc.<br>*Blidingia* present<br>*Cerithium* present (*c.* 50) |
| B | (Hornfels) | Uncaged | 80% *Calothrix* film, containing *Lyngbya*<br>20% *Ralfsia*<br>No obvious *Blidingia*<br>No fish toothmarks |
| | | Caged | 25% *Calothrix* mat containing *Arthrospira*, *Lyngbya*, *Microcoleus*, and *Blidingia*<br>50% film of *Calothrix* etc.<br>20% *Ralfsia*<br>5% *Blidingia*<br>*Cerithium* present (*c.* 20) |
| C1 | (St. Lucia tuff) | Uncaged | 70% *Calothrix* film*<br>30% *Ralfsia*<br>No *Blidingia* obvious<br>No fish toothmarks |
| | | Caged | 95% film of mixed spp. *Aphanothece* and *Monostroma* codominant, *Calothrix* and *Dermocarpa* present<br>5% *Blidingia*<br>*Ralfsia* present<br>*Cerithium* present (*c.* 100) |

* Additional species of blue-green algae almost certainly present.

# A STUDY OF THE DISTRIBUTION, HABITAT, BEHAVIOUR, VENOM APPARATUS, AND VENOM OF THE STONE-FISH

By R. Endean*

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*Summary*

Two species of stone-fish occur in Queensland waters. *Synanceja verrucosa* Bloch & Schneider is found on the Great Barrier Reef, whilst *S. trachynis* Richardson occurs in mainland waters.

*S. trachynis* is found commonly in sheltered bays and estuaries. It usually occurs partially embedded in mud or sand amidst weed-encrusted rubble, and it may be exposed to the atmosphere at low tide. The mean standard length of 52 specimens examined was 20·3 cm.

Twin venom glands are attached to each of the 13 stout dorsal spines which are normally covered by sheaths of tubercular skin. Venom production results from a holocrine type of secretion. Proteinaceous granules, 1·5–3·5 $\mu$ in diameter, are the end products of glandular activity. The venom ducts, which extend from the venom glands to the tips of the spines, are essentially attenuated portions of the glands. However, the ducts are enclosed within grooves in the spines and these grooves are spanned by dense collagenous fibres. The distal extremities of the grooves are plugged with connective tissue.

Only the tip of each spine can normally be protruded through the small aperture in its sheath. When a spine penetrates an object, such as a rubber sheet, the sheath is pushed down the tapering spine away from the tip of the spine and towards the twin venom glands. The sheath constricts the venom glands and, when sufficient pressure is transmitted to the intraglandular contents, the connective tissue plug at the distal end of the duct belonging to each gland tears. The intraglandular contents are thereby injected into the wound made by the spine.

Each spine must penetrate to a certain depth before expulsion of venom occurs. This depth depends on the distance of the attached glands from the tip of the spine. Small fish of standard length about 8 cm have a well-developed venom apparatus.

Regeneration of the intraglandular contents occurred after firing of venom glands in the one specimen where this regeneration was studied.

The contents of each gland are expelled in a single burst and the venom contains gland cells and venom granules. Dilute acid disrupts the venom granules.

## I. Introduction

The stone-fish (Plate 1, Fig. 1) has a grotesque appearance. Bony eminences, fleshy outgrowths, and deep concavities occur in the head region, and the trunk is studded with wart-like protuberances. Thirteen stout spines, normally covered with tubercular skin, overlie one another in the mid-dorsal line when the fish is undisturbed. These spines with their associated venom glands constitute the venom apparatus for which the fish is feared. There are few reports of stone-fish stings in Australian waters but the fish have caused a number of fatalities in the Indo-West Pacific area (Smith 1951; Halstead, Chitwood, and Modglin 1956).

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Stone-fish are common in certain areas along the Queensland coast and, because they are a potential danger to man, it was decided to investigate their distribution, habitat, and behaviour. It was also decided to investigate the histology of the venom and the venom glands and to ascertain the mode of action of the venom apparatus.

The histology of the venom glands has been discussed by Duhig and Jones (1928) and by Halstead, Chitwood, and Modglin (1956). However, Duhig's and Jones's account is incomplete and, in many respects, misleading. That of Halstead, Chitwood, and Modglin was based on formalin-fixed material and, as will be shown, formalin has a disruptive effect on the intraglandular material.

## II. Materials and Methods

In response to appeals for stone-fish made during the last three years, 38 specimens were received from various Queensland localities between Moreton Bay and Cairns. Some were captured on fishing lines, some were trapped in lobster pots, and others were caught in seine nets. Initially, the fish were dispatched to Brisbane in tins containing seawater and there were many casualties. Later, it was found that the fish arrived in good condition if placed in a box and surrounded only by moist sea-weed.

A further 15 specimens were collected by simply scooping them up with a hand-net from their hiding places amongst rubble on oyster leases in Moreton Bay. During collecting trips to Moreton Bay the habitat and behaviour of stone-fish were studied.

Some fish were placed in well-oxygenated seawater in aquaria, the floors of which had been covered with a layer of sand. The behaviour of these captive fish was studied.

The histological and histochemical techniques used in the investigation of the venom apparatus will be found under relevant headings.

## III. Distribution

Two species of stone-fish, *Synanceja trachynis* Richardson and *Synanceja verrucosa* Bloch & Schneider, have been recorded from Australian waters (Whitley 1943). Only one of 53 specimens of stone-fish collected or received by the author agrees with descriptions of *S. verrucosa*. This was collected at Heron Island in the Capricorn Group. Since this species has been recorded from regions in the tropical Indo-West Pacific area where coral reefs abound and has been collected previously in Queensland waters only from the Murray Isles and Batt Reef, it is possible that it is restricted to coral-dominated regions. It has now been recorded from both the northern and southern ends of the Great Barrier Reef and can be expected from intermediate localities.

On the other hand, 52 specimens of *S. trachynis* were collected in Queensland mainland waters. As the species has been recorded from Shark Bay and Port Headland in Western Australia and from Darwin in the Northern Territory it probably occurs throughout the mainland waters of tropical Australia.

Whitley (1930) pointed out that the Indian species *S. horrida* which closely resembles *S. trachynis* has been wrongly recorded from Australia.

The 52 specimens of *S. trachynis* obtained ranged from 7·8 to 29·0 cm in standard length with a mean standard length of 20·3 cm and a mean overall length of 24·7 cm.

## IV. Habitat

In Queensland, *S. trachynis* occurs in shallow water which is not subject to severe wave action. Thus, it occurs frequently in the numerous sheltered bays and estuaries which are found to the north of the biogeographical boundary at 25° S. (Endean, Kenny, and Stephenson 1956) but it is apparently absent from the wave-lashed shores found to the south of this boundary. It is, however, found in the sheltered waters of Moreton Bay (27° 30′ S.) which possesses an isolated tropical fauna (Endean 1953).

The preferred habitat of *S. trachynis* is a substratum of weed-covered rocks or rubble mixed with muddy sand. The oyster leases in Moreton Bay where oysters are farmed on rocks are much frequented by stone-fish. Specimens have not been observed on purely sandy areas nor have they been observed on mud flats which are devoid of rubble.

Although they will tolerate a reduction in salinity, since they have been collected in Moreton Bay from areas where the salinity averages about half that of normal seawater, stone-fish do not appear to penetrate any distance up rivers.

## V. Behaviour

Stone-fish are very sluggish. *S. trachynis* has adopted the habit of lying motionless in a slight depression in muddy sand surrounded by weed-encrusted rocks and rubble. It is extremely difficult to detect in its natural habitat unless a glimpse is obtained of the yellowish-green lining of the buccal cavity framed in the crescentic slit of the fish's upturned mouth.

When approached, it will not move. The dorsal spines are usually not raised until the fish is actually touched. It is possible, if wearing suitable foot-gear, to stand on the fish and prevent the spines being raised.

If picked up and returned to the water it will usually not attempt to swim off but will settle on the substratum immediately below the point where it is dropped into the water. When settling on the substratum, the stone-fish usually makes a shallow depression by scooping up sand or mud with its pectoral fins. Often the sand is piled up around the sides of the trunk, and the tail and pectoral fins are covered by a film of sand (Plate 1, Fig. 2). Thus concealed, the fish awaits its prey—usually small fish or crustaceans.

It was noted that the algae which frequently cover the skin of the fish are always the same colour and apparently of the same types as those in its immediate surroundings. This algal covering helps the fish to blend with its surroundings. It seems likely that the sticky milky fluid produced by the wart-like outgrowths of the skin is responsible for forming a film, to which algae adhere, over the fish. It is necessary to remove this film before the true colours of the fish can be seen.

At periods of low water, stone-fish are often left partially exposed by the retreating tide. At such times they may be surrounded only by a small quantity of water which fills the depression in which each lies and the main mass of water may be a considerable distance away. They can survive long periods (at least 24 hours) out of water providing their surroundings are kept moist.

When kept in aquaria, the floors of which were covered by a layer of sand, stone-fish often remained motionless (except for slight respiratory movements) in the same spot for several days. Occasionally, they were observed to swim slowly, using their pectoral fins as the main organs of propulsion. If approached whilst swimming, they frequently turned their bodies so that their dorsal spines pointed towards the intruder. Sometimes they feigned death by floating upside down, motionless, with their tails curled against their bodies.

Additional data on the behaviour of stone-fish will be found in publications by Saville-Kent (1900), Whitley and Boardman (1929), and Whitley (1932).

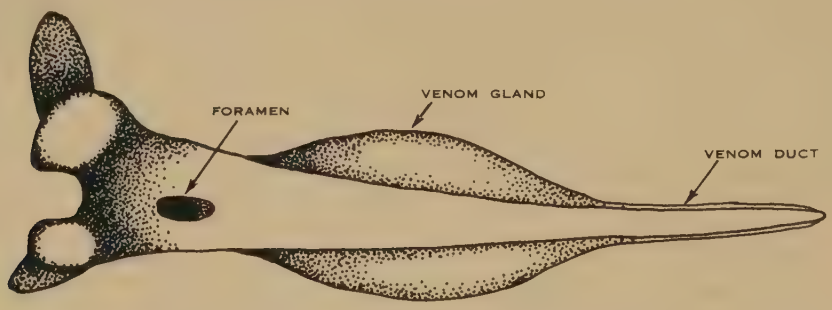


Fig. 1.—Drawing of posterior view of first dorsal spine, showing twin venom glands. The integumentary sheath has been removed. ×4.

## VI. The Venom Apparatus

### (*a*) *Anatomy*

The anatomy of the venom apparatus of *S. trachynis* has been adequately described by Duhig and Jones (1928) and by Halstead, Chitwood, and Modglin (1956). Although the latter workers have shown that venom glands are attached to three anal and two pelvic spines, these spines are completely enclosed by their sheaths and they appear to be non-functional as venom organs.

Essentially, the venom apparatus consists of 13 dorsal spines and their associated venom glands. Each spine, which tapers distally to a sharp point, possesses two lateral grooves, one on either side. Each groove partially accommodates a fusiform venom gland (Fig. 1). The glands are attached to the spines by connective tissue. Proximally, the connective tissue surrounding each gland thickens to form a tendon-like band which anchors the gland to the lower portion of the spine. Distally, each gland is attenuated to form a duct which runs to a point near the tip of the spine. At the proximal end of the spine are two lateral condyles separated by a median foramen. A semicircle of bone arising from the dorsal aspect of each interneural spine passes

through the median foramen of the corresponding dorsal spine. Duhig and Jones (1928) have described the muscles which raise and lower the dorsal spines.

When the dorsal spines are erected, the first three spines are vertical, or almost so, whilst the remaining spines are inclined towards the posterior end of the fish.

Measurements were made of the lengths of dorsal spines and associated venom glands and ducts from 12 specimens of *S. trachynis* with standard lengths ranging from 78 to 290 mm. The data obtained are embodied in Figures 2 and 3. When determining spine length, the distance between the tip of a spine and its articulating surface was measured.

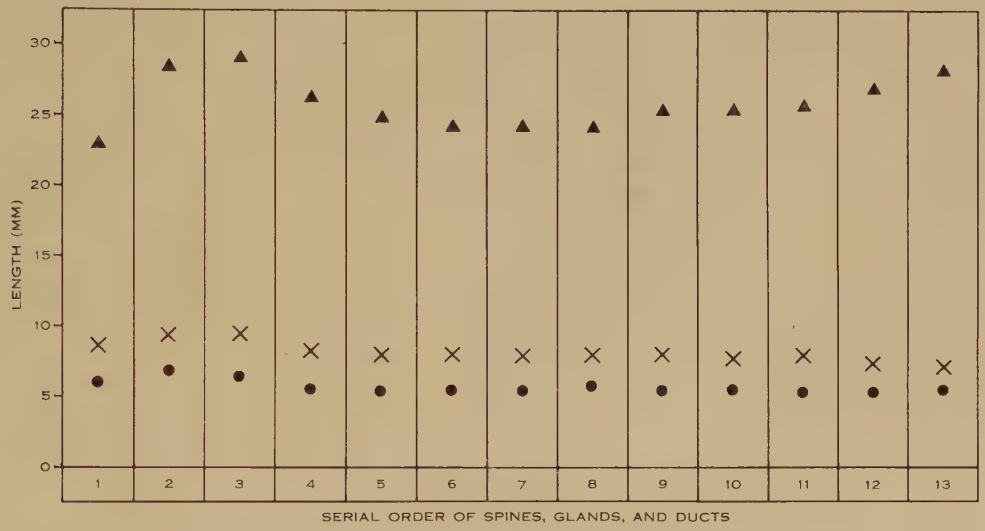


Fig. 2.—Relationship of average lengths of spines, glands, and ducts to their serial order. ▲, Spine; ×, gland; ●, duct.

As indicated in Figure 2, the first spine is the shortest and the third spine usually the longest of the 13 spines possessed by each fish. The ratio of standard length of fish to maximum spine length was approximately 6 : 1 in each of the 12 specimens examined.

There is a tendency for the glands attached to the first three spines to be slightly longer and for the glands attached to the last two spines to be slightly shorter than those attached to the other spines. The latter glands are remarkably uniform in size in each fish. The diameters of the venom glands ranged from approximately 1 mm in the smallest fish to approximately 3 mm in the largest fish measured.

The ducts of the first three spines are usually slightly longer than the ducts belonging to the other spines but differences in the lengths of ducts in each fish are small. However, even in the largest fish examined the ducts were not longer than 1 cm.

As can be seen from Figure 3, the ratios of gland length to spine length and of duct length to spine length decrease as the standard lengths of fish increase. Thus the glands are situated more distally on the spines of large fish than they are in small fish.

Average-sized fish, 20 cm in standard length, possess venom glands of the order of 1 cm in length and 2 mm in diameter and venom ducts about 7 mm in length. It is noteworthy that even fish as small as 7·8 cm in standard length possess a well-developed venom apparatus.

Some fish received possessed two or more venom glands which were merely empty sacs. In many cases, the spines to which these glands were attached protruded through their respective sheaths. It is believed that these glands had recently been discharged.

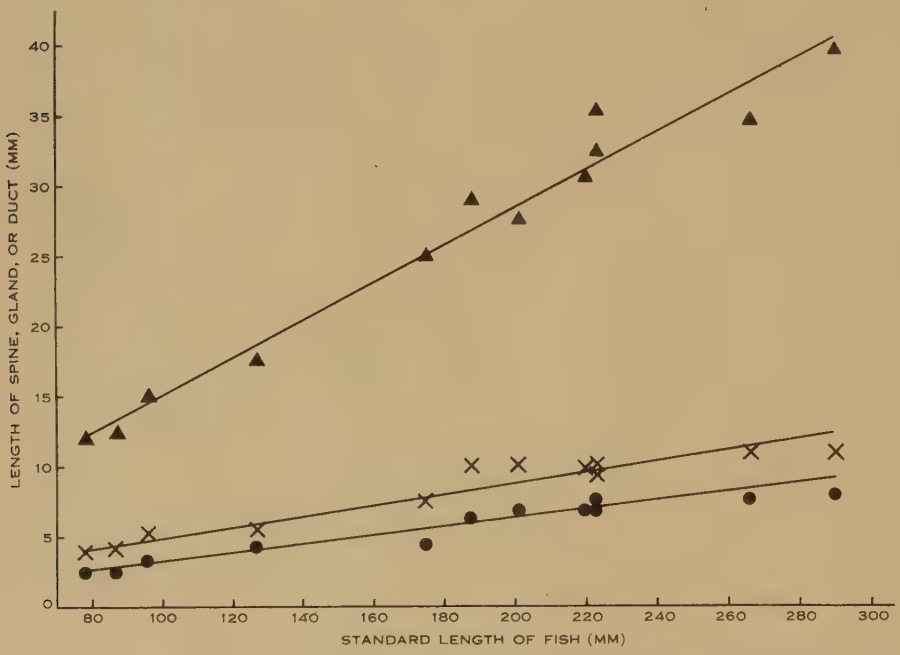


Fig. 3.—Relationship of average lengths of spines, glands, and ducts to standard length of fish. ▲, Spine; ×, gland; ●, duct.

### (*b*) *Histology*

The first three dorsal spines with their attached glands and sheaths were removed from each of three specimens of living stone-fish of approximately the same standard length (about 17 cm). Venom glands were exposed by removing the sheaths, and detached from their spines by paring away the bone which partially encloses each gland. The glands were then fixed variously with Bouin's fluid, Zenker's fluid, and 5% formalin in seawater. Transverse sections, 10 $\mu$ in thickness, were taken at intervals along the length of each of six glands. Serial transverse sections were made in the case of one gland fixed with Zenker's fluid, and longitudinal sections were taken from other glands.

The second dorsal spine with its glands and sheath was removed from each of two fish of standard lengths 19 and 20 cm and placed in Zenker's fluid. After fixation, each spine was decalcified with Gooding's and Stewart's fluid. Transverse serial

sections passing through the sheath, through the ducts or glands (depending upon levels at which the sections were cut), and through the spine were then made.

Sections were dyed with haematoxylin/eosin or with Mallory's dye mixture. Some sections were subjected to histochemical tests. Polysaccharides were sought by using the PAS reaction (Hotchkiss 1948; McManus 1948), lipids by Sudan black B, following the procedure outlined by Pearse (1960), proteins by the mercuric-brom phenol blue method (Mazia, Brewer, and Alfert 1953), and by Millon's reagent (Bensley and Gersh 1933). The localization of DNA was followed by utilizing the Feulgen reaction (Feulgen and Rossenbeck 1924), and that of RNA by using 0·001% ribonuclease in conjunction with Unna's methyl green/pyronin dye mixture as described by Pearse (1960).

Verhoeff's elastic stain, Hart's modification of Weigert's elastic stain, and the Taenzer–Unna orcein method were used to demonstrate elastic tissue. These stains were prepared and used in accordance with the procedures outlined by Culling (1957). The aldehyde–fuchsin stain of Gomori (1950) was also used to demonstrate elastic tissue.

A layer of densely fibrous connective tissue, 12–15 $\mu$ in thickness, formed the boundary of each gland. The fibrillar material was collagenous and it enclosed a mosaic of gland cells and granule-filled compartments (Plate 2, Figs. 1 and 2). Often, the cells were subcircular in outline and such cells had an average diameter of 36 $\mu$ with a range from 28–52 $\mu$. Frequently, however, when the cells were grouped in clusters, they each had a pentagonal or hexagonal outline, owing to adjacent cells abutting on one another.

Eosin dyed the cytoplasm of the cells pink to red, Mallory's dye mixture dyed them purplish to reddish. Presumably, the behaviour of the cells to these dyes is influenced by the stage each had reached in its secretory cycle. A positive PAS reaction was given by the cytoplasm and it exhibited $\beta$-metachromasy with toluidine blue. Much of this metachromasy was due to RNA. With Sudan black B the cells gave a faint reaction for lipid. When spherical, the cell nuclei averaged 6 $\mu$ in diameter. However, some nuclei were ellipsoidal and in some of the smaller cells nuclei undergoing division were observed. Nuclei were dyed faintly by haematoxylin and scarcely at all by Mallory's dye mixture. They were dyed by orcein and they were clearly revealed by the Feulgen technique.

The granule-filled compartments (Plate 2, Figs. 1, 2, and 3) were roughly circular in outline and they had an average diameter of 65 $\mu$. The walls of the compartments appeared to possess very fine branching fibres and minute pores but the lodging of large numbers of granules against these walls made observations of their structure difficult. Frequently, the walls of adjacent compartments had fused, possibly owing to the action of the fixatives used, and it was thought, initially, that the granules were enclosed in a meshwork which ramified throughout the gland. However, close study of both longitudinal and transverse sections revealed that the granules were enclosed in spherical compartments which abutted on gland cells, other compartments, and, when at the periphery of the gland, on the collagenous walls of the gland.

Collagenous material was not present in the walls of the compartments as these were not dyed by the aniline blue component of Mallory's dye mixture. Although they stained heavily with Verhoeff's and Gomori's elastic tissue stains, variable results were obtained when the Taenzer–Unna orcein method for elastic tissue was employed. Bouin-fixed material gave a positive result. Zenker-fixed material gave a negative result, the dye being removed from the tissue by 70% alcohol. Negative results were obtained when Weigert's elastic tissue stain was employed.

The granules (Plate 2, Fig. 3) present in the meshwork were often irregular in shape, but when subspherical they had diameters ranging from 1·5 to 3·5 $\mu$. They were strongly eosinophilic, were dyed orange by Mallory's dye mixture, and were dyed black by Verhoeff's elastic tissue stain. They gave a positive reaction only for protein with the histochemical reagents used. Counts of granules in each of ten randomly selected compartments apparent in a 10-$\mu$ section gave figures which ranged from 72 to 264.

It was established that the granules were produced by the gland cells. Many of the larger (greater than 35 $\mu$ in diameter) gland cells contained vacuoles with diameters ranging from 3 to 6 $\mu$. In these vacuoles, granules often occurred in small clusters (Plate 2, Fig. 4). The granules were dyed orange by Mallory's dye mixture whilst the rest of the cell was dyed reddish to purplish. Also, the vacuolar contents were dyed strongly by Verhoeff's elastic tissue stain. Although the nucleus of each cell was coloured by this stain, the rest of the cell was not coloured. Some cells were packed with vacuoles and it was difficult to distinguish these cells in sections from compartments in which the granules were tightly packed. It was evident that compartments containing granules are the end products of the development of gland cells. The cytoplasm of the vacuole-packed cell disintegrates and the vacuoles break down to liberate their contained granules although the liberation of the granules from the vacuoles was not detected in the sections examined. Possibly the fixatives used disrupted the vacuoles of the gland cells which had reached a late stage in their development. The gland cell walls form the boundaries of the compartments. Judging by the reactions of the boundaries of the compartments to stains, particularly elastic tissue stains, the chemical constitution of the gland cell walls must be modified during their later stages of development.

Some glands appeared to contain more granule-filled compartments than other glands but otherwise no marked differences were observed in the structure of the glands examined. Moreover, the structure was essentially the same from distal to proximal ends of the same gland.

Bouin and Zenker fixation yielded similar histological pictures but formalin fixation caused shrinkage and vacuolization of cells, tearing of the walls of compartments, and resulted in the granules being transformed into an amorphous mass.

The glandular structure is preserved in the duct of each gland (Plate 3, Figs. 3 and 5) which is essentially a continuation of the gland. However, about 300 $\mu$ from the distal end of the groove in the spine glandular tissue ends abruptly against collagenous tissue which fills the distal extremity of the groove (Plate 3, Fig. 2).

Collagenous connective tissue is the principal constituent of the sheath surrounding each spine. This connective tissue is separated from an outer epidermis by a line of black pigment (Plate 3, Fig. 6). Immediately above the tip of each spine there is an aperture in the sheath of the order of 150 $\mu$ in diameter. Transverse sections passing through the tip of a spine (Plate 3, Fig. 1) show the connective tissue of the sheath in the vicinity of the spine to be denser than elsewhere at the same level, and the connective tissue fibres in this dense region tend to be disposed circularly around the spine. Connective tissue is applied to the surface of the spine and protrudes into the distal ends of the grooves in the spine. As the grooves deepen, the spine becomes roughly T-shaped in cross section and, about 120 $\mu$ from the distal ends of the grooves, densely fibrous connective tissue appears and spans the grooves in the spine. In each groove connective tissue possessing very fine fibres is enclosed. This tissue effectively plugs the distal end of the venom duct lying in the groove. Apart from a thin layer of this connective tissue which lines the grooves in the spines occupied by the venom ducts and glands, the walls of these ducts and glands are formed from the densely fibrillar connective tissue.

Cross sections of the spines show a series of fine concentric lines.

### (*c*) *Mode of Action*

It has been shown that the secretory granules produced by the gland cells are stored within each gland, and the question arises how the secretory products leave the glands.

Each dorsal spine is normally well covered with a sheath of tubercular integument. A small aperture through which the tip of the spine can be protruded is present in each sheath. When moderately stimulated, stone-fish raised their dorsal spines without these being protruded through their respective sheaths. Strong stimulation resulted in retraction of the sheaths and exposure of the tips of the spines. Duhig and Jones (1928) have described a muscle, the "panniculus spinae", which they believed responsible for retracting the sheaths from the tips of the spines. However, it is doubtful whether this muscle is responsible for the exposure of more than the tips of the spines. During the present investigation, fish were not observed to expose more than the tips of the dorsal spines.

Living stone-fish were pinned to a dissecting board by driving spikes through their pectoral fins. Pressure exerted with a pair of forceps on the region of the venom glands of each dorsal spine did not result in venom being expelled. The sheaths surrounding each spine were then dragged back with forceps towards the proximal ends of each spine. The aperture in the sheath through which the spine passes is very small and as the sheath was retracted from the tapering tip of the spine, the margin of the aperture tightened around the spine. As the sheath passed back over the venom glands of each spine, it constricted then stretched them until a point was reached when the contents of the glands were expelled with great force through the ducts leading from each gland to the tip of the spine. Only the empty sacs of the glands remained.

In another experiment, a rectangular rubber sheet, 2 mm in thickness, was pulled down over each dorsal spine in turn. The rubber was readily penetrated by

each sharp spine and the sheath surrounding each spine was dragged back towards the proximal end of the spine. A violent expulsion of venom from the twin venom ducts occurred after the sheath had first constricted and then stretched the venom glands.

In the above experiments about 0·1 ml of venom was released from the twin venom glands attached to each spine.

### (*d*) *The Venom*

Drops of freshly-expelled venom, which has the appearance of an opalescent viscous fluid, were placed on cover-slips and hanging drop preparations examined. Other drops of venom were exposed to osmium tetroxide vapour for 5 min before examination.

Each drop was packed with granules identical with those observed in sections of the venom glands and with gland cells present singly or in clusters. These cells were darkened with osmium tetroxide vapour. Most of the spherical compartments had burst, liberating their contained granules, and fragments of the walls of these compartments were noted. Thus all the intraglandular structures seen in sections of a venom gland were represented in venom drops.

Some collagenous fibres, presumably derived from the connective tissue which plugged the ends of the ducts, and occasionally nucleated blood cells which had diameters ranging from 9–12 $\mu$, were also observed.

A drop of fresh venom when exposed to air quickly formed a coagulum in which granules were no longer apparent. The addition of 5% formalin or a drop of 0·001N HCl to a drop of venom resulted in the immediate formation of a similar coagulum.

### (*e*) *Regeneration of the Venom Apparatus*

One stone-fish of standard length 18·3 cm was returned to an aquarium after the venom had been expelled from the venom glands attached to three spines as described in Section VII. After 3 weeks the fish was killed and sections taken through the venom glands of the three spines. It was apparent that regeneration of the contents of each gland had occurred. However, the collagenous sheath of each gland was much folded, and most of the gland cells were small as were the compartments containing granules. Moreover, the ratio of gland cells to compartments with granules was far greater than in fully developed glands. These observations, although made on only one specimen of stone-fish, suggest that regeneration of the contents of venom glands can occur within 3 weeks.

## VII. Discussion

The venom apparatus of *S. trachynis* is a defence mechanism. The dorsal position of the apparatus coupled with the habit of the stone-fish of lying partially embedded in the substratum would seem to be well suited to foiling the attacks of predatory animals. Moreover, it would appear that the expulsion of the venom cannot be directly controlled by the fish. The absence of muscular tissue within the venom glands and its virtual absence from the sheaths, the storage within the

glands of the products of secretion of the gland cells, and the results of experiments and observations made on the mode of discharge of the venom apparatus all militate against the assumption of a direct control of venom expulsion by the fish.

It has been found that pressure must be exerted on the integumentary sheaths surrounding the dorsal spines before the venom is expelled. Such pressure would be exerted when an animal, human or other, impales itself on the spines. The sheath of each spine involved would then be pushed towards the proximal end of the spine as the spine enters the victim's flesh. Since the sheath possesses only a small aperture through which only the tip of the spine can be protruded normally, the sheath, as it passes back along the tapered spine, constricts the venom glands which are found towards the mid region of the spine. Dense collagenous tissue is present in the sheath and collagenous fibres are resistant to tensile strains. This is of importance if the sheath is to constrict the glands.

Constriction of the venom glands which are firmly attached to each spine would result in pressure being transmitted to the intraglandular fluids. This pressure would increase as the glands themselves are stretched towards the proximal end of the spine. The wall of each venom gland is comprised of very dense collagenous fibres which prevent the glands from bursting. The only possible route for the ejection of the intraglandular material is via the duct leading from each gland to the tip of the spine to which it is attached. When sufficient pressure is built up inside each gland, the connective tissue plug at the end of its duct tears and the contents of each gland are expelled violently through its duct and thereby injected into the wound made by the spine to which the gland is attached.

Gland cells as well as secretory granules are ejected but it is probable that some gland cells remain and permit regeneration of the intraglandular material to occur, as happened in one specimen where regeneration of three pairs of venom glands was studied.

It is noteworthy that the venom from the twin venom glands of each spine is expelled in a single burst and that the venom is expelled only after the spine to which they are attached has penetrated to a certain depth. The depth of penetration required would vary from about 0·6 cm in the case of a small fish about 12 cm in standard length to about 1·0 cm in the case of a fish about 26 cm in standard length. Even in the smallest fish examined (7·8 cm in standard length) the spines and venom glands were well developed.

Venom production is the result of a holocrine type of secretion and the secretory products are in the form of granules. It would appear that the smaller, less highly developed gland cells reproduce themselves throughout the glands and ducts. No basal layers of proliferating cells occurred in the glands or ducts and no recruitment of cells from outside the glands or ducts was observed. Venom granules developed only in the larger cells with diameters in excess of 35 $\mu$ and presumably the smaller cells with diameters between 28 and 35 $\mu$ provide a pool of undifferentiated cells. Some of these smaller cells appeared to be undergoing division in some sections. However, apart from the lack of granules or their precursors, there are no obvious structural features which serve as a basis for distinguishing the undifferentiated cells

from the smaller of the cells containing granules or their precursors. Also, venom production occurs in similar fashion throughout the glands and ducts and there are no consistent differences in the degree of differentiation of the secretory cells at different levels throughout the glands and ducts as there are in mammalian glands such as sebaceous glands.

The behaviour of the gland cells which have become packed with secretory granules to dyes, particularly elastic tissue dyes, suggests that the chemical constitution of the gland cell walls alters during the development of these cells. However, it is unlikely that elastin is formed in the walls of these cells. The secretory granules which lodge in large numbers against the walls of these cells are also dyed by certain of the elastic tissue stains, particularly those of Verhoeff and of Gomori, and it is possible that some secretory products are adsorbed by the gland cell walls.

The chemical nature of the proteinaceous secretory granules has not been determined, but these granules are the end products of glandular activity. They do not seem to have been observed previously. Halstead, Chitwood, and Modglin (1956) who have reviewed the literature on the venom glands of synancejids make no reference to them. These authors (p. 390) believed that clusters of "tan bodies" observed in sections of the venom glands represented the areas of venom production and they referred to "patches of yellowish, homogeneous, amorphous secretion" scattered amongst the tan bodies. It would appear that these authors are dealing with artefacts owing to the use of formalin as a fixative. The "tan bodies" probably represent shrunken gland cells and the patches of amorphous secretion probably represent venom granules disrupted by the fixative used.

Wiener (1959) observed in the fresh venom of *S. trachynis* cells 30–40 $\mu$ in diameter and more numerous cells measuring 10–12 $\mu$ in diameter. The larger cells are undoubtedly gland cells but the smaller cells appear to be blood cells.

The secretory granules are present in the freshly expelled venom and they will be injected into the wounds caused by the spines of the fish if these spines penetrate the requisite distance to cause discharge of the attached venom glands. Of interest is the immediate disruption of the venom granules by dilute acid. Wiener (1959) found that the toxicity of stone-fish venom was destroyed if its pH was brought below 4, and he suggested (amongst other methods of treatment) the injections of acid solutions into the punctures caused by stone-fish spines. It would seem, that as well as disrupting the granules, acids must alter the chemical structure of the granules in such a way as to render them non-toxic.

It has now been shown that the venom can be "milked" from the venom glands of stone-fish and investigations are proceeding to test the efficacy of the injection of readily available dilute acids in the treatment of stone-fish stings.

## VIII. Acknowledgments

The author wishes to thank the many people who have forwarded living stone-fish. The assistance given in the organizing of collections by Dr. J. Barnes of Cairns, Dr. R. A. Rimington and Mr. R. Kenny of Townsville, Mr. E. Stewart of Magnetic Island, Superintendent D. L. G. Williams of Mackay and the Managers of *The Bowen*

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## Explanation of Plates 1–3

### Plate 1

Fig. 1.—Photograph of stone-fish, *S. trachynis*.

Fig. 2.—Photograph of *S. trachynis* (inside white circle) in its natural habitat. The fish is covered by about 2 in. of water and is partially embedded in the substratum. It possesses a coating of algae and blends in well with the weed-encrusted rubble in its surroundings.

## Plate 2

Fig. 1.—Photomicrograph of section of venom gland of *S. trachynis*, showing gland cells and granule-containing compartments. The gland was fixed in Zenker's fluid and the section was dyed with Mallory's dye mixture.

Fig. 2.—Photomicrograph of section of venom gland of *S. trachynis*, showing gland cells, granule-containing compartments, and part of wall of gland. The gland was fixed with Zenker's fluid and stained with Verhoeff's elastic tissue stain.

Fig. 3.—Photomicrograph of section of venom gland of *S. trachynis*, showing compartments containing venom granules. The gland was fixed in Zenker's fluid and the section was dyed with Mallory's dye mixture.

Fig. 4.—Photomicrograph of gland cell containing two vacuoles with granules. The gland was fixed with Zenker's fluid and dyed with Mallory's dye mixture. Oil immersion.

## Plate 3

All figures are photomicrographs of material taken from *S. trachynis*, fixed with Zenker's fluid, and dyed with Mallory's dye mixture. The spines were decalcified with Gooding's and Stewart's fluid.

Fig. 1.—Section through sheath and tip of spine.

Fig. 2.—Section showing connective tissue plugs in the distal ends of grooves in spine and the sheath in the immediate vicinity of spine.

Fig. 3.—Section through sheath, venom ducts, and spine.

Fig. 4.—Section through sheath, spine, and twin venom glands.

Fig. 5.—Section through spine and ducts showing gland cells and compartments with granules within ducts. Note the densely fibrous connective tissue spanning one of the grooves in the spine.

Fig. 6.—Section through portion of sheath at level of venom glands showing connective tissue in sheath and the line of black pigment separating connective tissue from the epidermis. Part of a venom gland is visible.

A STUDY OF THE STONE-FISH

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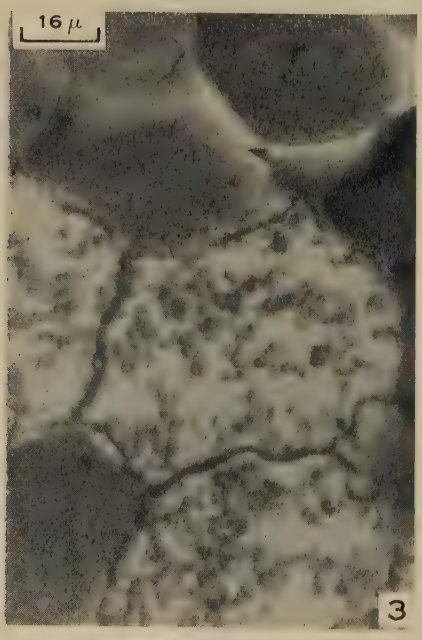

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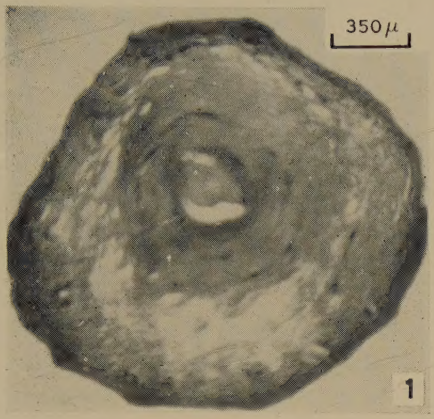


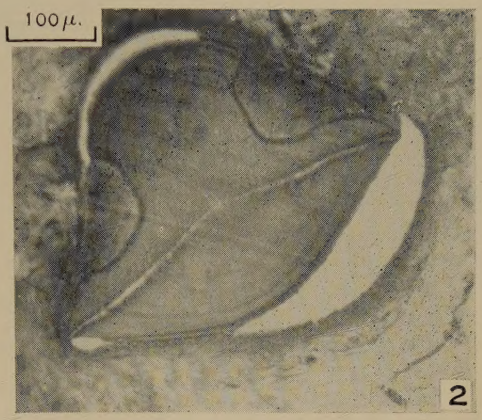


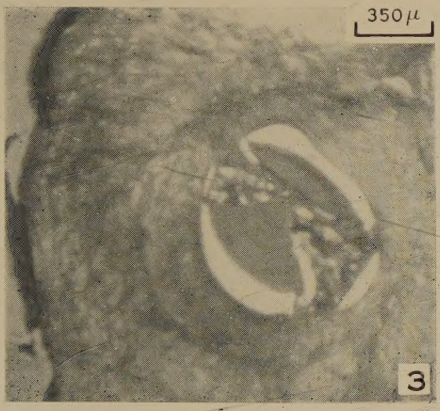


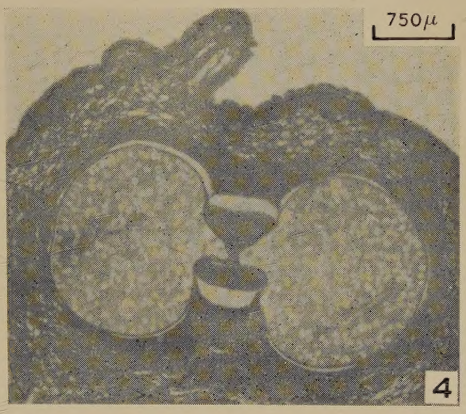


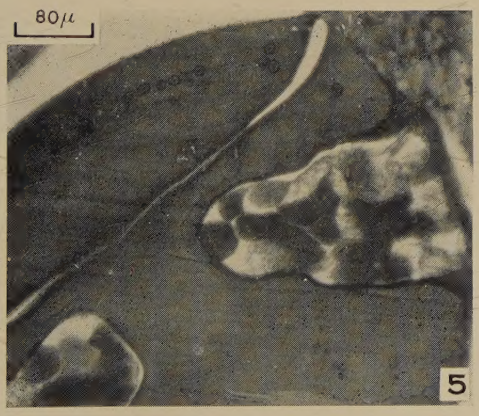


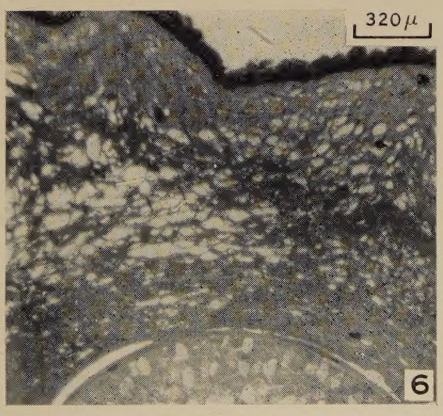

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